EFFECTS OF THE LOUISIANA CRAYFISH (*PROCAMBARUS CLARKII*) INVASION ON THE FOOD AND TERRITORIAL ECOLOGY OF THE AFRICAN CLAWLESS OTTER (*AONYX CAPENSIS*) IN THE EWASO NG'IRO ECOSYSTEM, KENYA.

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This thesis is my original work, and has not been presented for a degree in any other University or any other award.

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DEDICATION

To my wife Darcy, for all your encouragement, support and help during this work. To Mum, Arthur, Joshua, Harriet, Tanja, Julie & Junior for being a wonderfully supportive family. Thank you all for always being there for me. In memory of Dad, who inspired me to become a scientist.
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ABSTRACT

The introduction of the Louisiana red swamp crayfish (Procambarus clarkii Girard) into the Ewaso Ng’iro river ecosystem has been one of the most profound human impacts on this system in recent years. The crayfish has spread throughout the lower Ewaso Ng’iro, becoming a new food source, competitor and predator to various organisms at different levels in the food chain. This was a two-year study covering two complete long and short rainy seasons as well as the intervening dry seasons. The study also aimed to provide information on the status of the African clawless otter (Aonyx capensis Schinz, 1821), which is unknown in much of its range. The study examined the impacts of the crayfish invasion on the African clawless otter and its primary food source, the indigenous freshwater crab (Potamonautes neumannii), which are predators and competitors to the crayfish, respectively. Trap sampling indicated that crayfish have supplanted indigenous crabs in much of the lower Ewaso Ng’iro River north of the equator. This was confirmed by experimental competition between captive crabs and the crayfish, where crabs in a tank without refuges were killed significantly faster (mean diff=56, ‘t’ value=9.058, df=9, p<0.0001) than those in the tank with rocks for refuge. Crayfish are excluded from the upper Ewaso Ng’iro and its tributaries south of the equator by low water temperatures. Since the crayfish forms such a large proportion of the otter’s diet, results of this study showed that the environmental factors affecting the crayfish also influence habitat use by otters. This was investigated mainly by collection of otter faeces within the study area and laboratory analysis of the same. Territorial behaviour of the otters was inferred from the distribution of the faecal deposits. Temperature and depth of water were measured to deduce the effects of these factors on the river ecosystem, within which the otters are functioning as tertiary consumers. The above abiotic factors are influenced by human impacts such as siltation, water extraction and construction of reservoirs. This study has shown that the territorial behaviour (marking frequency) of otters in the Ewaso Ng’iro ecosystem is significantly lower (mean diff = -30.158, df=11, ‘t’ value = -5.030, p<0.0005) in areas that have been invaded by the Louisiana crayfish than in the pristine (crab) areas. Crabs were found to contain significantly higher protein content per unit live weight than crayfish (mean diff = 7.449, df=19, ‘t’ = 17.281, p<0.0001). Consequently, carrying capacity for otters was also reduced by the invasion and density was significantly higher (mean diff = 5.198, ‘t’ value = 10.958, df=11, p<0.0001) in the pristine areas. Trap sampling showed a 75% reduction in diversity of the sampled segment of aquatic fauna during the study period.

This study recommends how best people can exploit river ecosystems with minimum effect on aquatic fauna. This aspect urgently needs attention because currently, there is no regulation on the introduction of alien species, and sport fishermen continue to stock aquatic ecosystems with exotic species without any due consideration to the ecological impacts of these activities.
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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

The main threats to aquatic systems worldwide include chemical and thermal pollution and invasive species. The ecological effect of biological invasions on ecosystems tends to be even more acute than chemical pollution, which can be eliminated at the source point (Allan, 1995). Alien species reproduce and disperse beyond the point of origin, and their effects are largely irreversible (Allan, 1995). Over 160 species of exotic fishes are listed as invasive in 120 different countries by the United Nations Food and Agriculture Organization (FAO) (Allan, 1995). During the nineteenth century and the first half of the twentieth century, fish introductions occurred largely as a consequence of colonialism and nostalgia by settlers for species left behind in their homelands (Welcomme, 1984). This is what appears to have happened in the case of Kenyan fish introductions. Other reasons for introductions include aquaculture, improving fisheries, and control of other fishes (Pitcher & Hart, 1995).

The Large mouth bass (*Micropterus salmoides*) was introduced from North America into Kenya (Lake Naivasha) in 1929 by sport fishermen. Shortly thereafter, the bass were found to be depleting other fish species in the lake by predation. The Louisiana red swamp crayfish (*Procambarus clarkii*) was later introduced to provide food for the bass. The crayfish became the most important food item for the bass, comprising up to 77% of bass diet (Siddiqui, 1977, Aloo & Dadzie, 1995), but depending on the availability of other food items, this proportion can decline to 28% (Aloo, 1988). The Louisiana crayfish was later discovered to be an aquacultural "cash crop" and was spread through various freshwater ecosystems as people sought to profit from it. Kenya now exports over 6,000 kg of crayfish.
annually (Fisheries Department Annual Report, 2002). However, it was never fully accepted locally as a food item, and has been regarded as a pest (Holdich & Lowery, 1988). It was also found to be a potential biological control agent for natural populations of schistosome transmitting snails (Mkoji et. al., 1992), and this further accelerated the spread as people sought to eliminate the disease vector snails. Introductions of North American crayfish into many countries, including Europe, have caused many changes in freshwater ecosystems, including reductions in plants, native crabs, fishes, and native crayfish. The local extinction of native European crayfish has resulted primarily from fungal plague (Aphanomyces astaci), which is endemic to many North American crayfishes but lethal to other crustaceans (Alderman, 1996). Other mechanisms of impact on native crustaceans include interspecific competition for shelter and food, often making the native species more vulnerable to predators (Lodge et. al., 2000).

The Louisiana crayfish (Procambarus clarkii) has invaded the lower Ewaso Ng’iro river north of 37°N 0280567 UTM 0014892 and has supplanted the indigenous freshwater crab (Potamonautus neumannii) in shared habitats. Kruuk and Goudswaard (1990) analyzed otter faecal pellets from the Ewaso Ng’iro river and found them to consist almost entirely of remains of crabs and an ‘unidentified crayfish’ This indicates that crabs were widespread in the Ewaso Ng’iro river prior to the crayfish invasion and still persisted until 1990. The crayfish has, therefore, replaced the freshwater crab as the main component of otter diet in the lower Ewaso Ng’iro. This study examines the effect of this shift to a new food base on the territorial behaviour and ecology of the African clawless otter. In this chapter, the existing information on the status of this species and its prey base in the Ewaso Ng’iro ecosystem has been reviewed. This information has been used to formulate the present study whose rationale, objectives and hypotheses are provided at the end of the chapter.
1.2 LITERATURE REVIEW

1.2.1 The African Clawless Otter

The African clawless otter (*Aonyx capensis*) (also known as the cape clawless otter) is a large aquatic carnivore measuring 1 to 1.6 meters in length and weighing, on average, 10 to 18 kg (Kingdon, 1997). It is one of 13 species in the sub-family Lutrinae of the family Mustelidae. It is mainly crepuscular but activity has been recorded at all times of day or night. It is a highly adaptable animal, but in habitats with heavy human presence, it is completely nocturnal (Estes, 1991). The otter has underdeveloped vestigial claws on its digits (Kingdon, 1997), which make it very difficult to catch fish, leading to the high dependence on crustacean prey. The forefeet are unwebbed and specialized for probing and manipulating (Plate 1), with a hairless underside and opposable thumb (Estes, 1991).

Both male and female clawless otters establish territories on which they remain for long periods, using a series of dens (Kingdon, 1989). They live in family groups of 4-6 individuals, which defend a common territory of 3-20 km of river (Kingdon, 1997). In marine environments, 'clans' of up to 6 adult males were reported to share territories and even forage together (Arden-Clarke, 1986). The African clawless otter is known to dig its own dens or holts (Mason & MacDonald, 1986) under the roots of trees along river banks. The family bonds in riverine habitats are temporarily broken during the reproductive season, because female otters are extremely intolerant of other otters during gestation and before the cubs are old enough to leave the den (Estes, 1991). This behaviour was also observed in captive otters at Toledo zoo in Ohio, U.S.A. (Randi Meyerson-McCormick, pers. comm.). Female otters are very aggressive in the defense of their young (Kingdon, 1997) and are known to kill large dogs by dragging them under water and drowning them (Harris, 1968).
Plate I. The African clawless otter (*Aonyx capensis*)
Trapped otters display extreme aggression (pers. obs.) further confirming the view that pound for pound, they are arguably the most formidable African carnivore (Estes, 1991).

In the Ewaso Ng’iro drainage, preliminary surveys in the relatively pristine Burguret study area indicate that this ecosystem initially had a stable otter population, although they were rendered vulnerable by the size of the prey species they depend on. Even in this area, where the otters are relatively successful, they are seldom seen, and consequently are unknown to most of the people in the area. This low visibility corresponds to the profitability of prey species because where prey species are small, like in the Burguret river, otters spend practically all their active hours foraging. This is mostly done swimming under water with the body held at a 45-degree angle while the otter searches the riverbed by touch using its forefeet (Rowe-Rowe, 1977b), so it would be visible only when it surfaces to breathe. This is in contrast to otter populations living in Tsitsikama National Park on the rocky coastlines of the Eastern Cape in South Africa, which feed on prey species that are up to 5 times as profitable as *Potamonautes neumannii* (Plate 2) or *Procambarus clarkii* (Plate 3). They were visible enough for sightings by hikers passing through the park to be used as a source of scientific data (Van der Zee, 1982). This can be taken as an indicator of success in otter populations because they are seen only when they are engaged in play, rest, or territorial marking behaviour. A high probability of sightings by transient people (hikers) reflects much higher success than populations that are not visible even to resident people (Mason & MacDonald, 1986).
Plate 2. The freshwater crab (*Potamonautes neumannii*)

Plate 3. The Louisiana crayfish (*Procambarus clarkii*)
1.2.1.1. Distribution and status of the African clawless otter

The African clawless otter is widely distributed in sub-Saharan Africa in permanent rivers, streams, swamps and lakes at altitudes from sea level to 3,000 meters (Kingdon, 1997). They also inhabit rocky coastlines in South Africa (Van der Zee, 1982). The major gap in their range is the central Zaire basin, which is occupied by the Congo clawless otter (*Aonyx congicus*). However, there are a few areas in Western Uganda, Western Tanzania, and Northern Congo where *A. capensis* and *A. congicus* overlap (Fig. 1). Davis (1978) considered *A. congicus* to be a subspecies of *A. capensis*, but genetic work done thus far has been insufficient to either refute or support this argument.

The African clawless otter is not listed by the International Union for the Conservation of Nature (IUCN) as endangered or threatened, but this is more likely to be an indication of data deficiency, rather than the overall condition of the population. Literature searches indicate that by December 2004, there were approximately 20 published research papers available on the ecology and behaviour of (*A. capensis*). Of these, 18 were based on research work done in South Africa, and 2 were based on research done in Rhodesia (now Zimbabwe). The areas studied thus far, therefore, comprise less than 20% of the known geographical range of this species according to Kingdon (1997). Even this area is not comprehensively covered because the work done by Rowe-Rowe (1977a, 1977b), Van der Zee (1981), Arden-Clarke (1986) and Somers (2000) is biased towards the ecology of otters in coastal (marine) and estuarine habitats. This work is, therefore, the first in-depth ecological study of *A. capensis* north of Zimbabwe. Mason and MacDonald (1986) made the only attempt to get an exact picture of the status of otters in Africa by contacting zoologists and conservationists throughout their known range (25 countries). Otters were found to be distributed as follows: Absent in 3 countries, very rare in 4 countries, rare in 9
countries, and fairly common in 9 countries. Otters were not considered common in any of the countries (Mason & MacDonald, 1986).

1.2.1.2. Occurrence of otters in the study area

The earliest recorded sighting of the African clawless otter in the Laikipia Plateau was in 1883 (Thomson, 1885). The first record of crayfish in the Ewaso Ng’iro river is from otter scats analyzed by Kruuk and Goudswaard (1990) and based on the proportions in otter scats, it can be estimated that the introduction occurred not more than 20 years ago (around 1985). It can, therefore, be assumed that otters preceded the Louisiana red swamp crayfish in the Ewaso Ng’iro ecosystem. It is the largest predator in the upper Ewaso Ng’iro river ecosystem. Other prominent predators being the marsh mongoose (Atilax paludinosus), fish eagle (Haliatus vocifer), darter (Anhinga rufa), goliath heron (Ardea goliath), monitor lizard (Varanus niloticus) and predatory fish such as the barbels (Barbus paludinosus). According to Kingdon (1989), the marsh mongoose is the nearest ecological competitor of the clawless otter, although it forages mostly in marshes and on the riverbank whereas the otter forages in deep water. Otters’ preferred hunting depth is 0.5 to 1.5 meters (Somers, 2000). This is, therefore, an important factor in determining otter distribution in shallow rivers such as the Ewaso Ng’iro.
Figure 1. Distribution of the African clawless otter (adapted from Kingdon, 1997)
1.2.1.3. Diet of the African Clawless otter.

The most frequent evidence of the presence of *Aonyx* is the dung deposits that consist mainly of crushed crab shells and catfish bones (Kingdon, 1997), although they also eat mollusks, small mammals and birds (Stuart & Stuart, 1997). Copley (1950) noted these otters eating young maize cobs and they may, therefore, also eat fallen fruit that are frequently plentiful along riverine habitats. However, crabs are the most important part of the diet of *Aonyx*. To avoid having their sensitive fingers bitten, the otters have developed a special technique for flipping the crabs over or out of the water, where they can be more easily eaten (Kingdon, 1989; Maxwell, 1960). The specialization of the otter’s hands for grasping and probing and of the teeth for crushing, are reflected in its prey preferences. Their manual dexterity has also been observed in their ability to use rocks to break open the shells of freshwater mussels (*Aspatharia wahlbergi*) in lacustrine habitats (Donnelly & Grobler, 1976). Given a choice of crabs, frogs and fish, a captive female always chose crabs first and frogs second, taking these in similar proportions as represented in the scats of wild otters (Rowe-Rowe, 1997b). Otters have been recorded to prey on lesser flamingoes (*Phoeniconaias minor*) in Kenya (Ruppell & Ruppell, 1980) but these two species have very different habitat requirements, so this would be a rare occurrence.

Otter scats collected over a 3-year period in Natal, South Africa contained 62% crab (*Potamonautes spp.*) remains and 8% fish (Rowe-Rowe, 1977a). It also contained some ungulate dung, insect, bird, frog, snake, and mollusk remains. This suggests that the otter’s dietary choices are highly influenced by availability of various food items, especially because hunting is mostly by touch in turbid water. Foraging in turbid waters is also aided by the long vibrissae (whiskers), which help the otter locate prey items. Consequently, analysis of the composition of otter faeces over time can be a reliable indicator of aquatic
community dynamics. Coastal otters took a wide variety of prey species, but four species accounted for over 80% of the diet. These were: two species of crabs, *(Plagusia chabrus)* and *(Cyclograpsus punctatus)*; octopus *(Octopus granulatus)* and a suckerfish *(Chorisochismus dentex)* (Mason & MacDonald, 1986).

1.2.1.4. Threats to the African clawless otter

Natural threats to otters include predation by the crocodile *(Crocodilus niloticus Laurenti)* which would prey on both adult and young otters in shared habitats (Procter, 1963). Kruuk and Goudswaard (1990) suggested that the African fish eagle *(Haliaetus vocifer)* may be a predator of otter pups in habitats like Lake Victoria, where fish eagle densities are high (1.5 pairs per Km of shoreline). Due to their low profile, otters do not suffer as much direct persecution as other wild carnivore species. Even where they were known, deliberate persecution of otters has historically been rare (Procter, 1963). Whenever they are found, otters are still locally killed for food and skins (Mason & Mac Donald, 1986). The skin trade problem has been mitigated by the fact that most African countries are members of CITES and prevent the uncontrolled trade in skins (Mason & MacDonald, 1986). Conflict between otters and humans has increased in recent years, particularly with the sport fishing fraternity. Brown trout *(Salmo trutta)* is an exotic species native to North America that was introduced to Africa in the early 20th Century by colonial settlers for purposes of recreational fishing (Allan, 1995). Trout breeding for sport fishing is a major economic activity in South Africa and trout breeders feel that otters threaten their livelihood by eating the trout. Therefore otters are routinely trapped and shot in these areas (Rogers, 2003). In nature, fish forms only 8% of the diet of *A. capensis* in Natal, South Africa (Rowe-Rowe, 1977a). However, the conflict may arise because trout bred in cramped hatcheries and
released into the wild are physically ill-equipped to escape from otters (Rogers, 2003), leading to an unnaturally high fish intake. This is the only recorded instance thus far of the African clawless otter population being indirectly threatened by the introduction of an exotic species into their habitat. The greatest threat to otters is the loss of their food base associated with increased human population, for example, overgrazing and deforestation, which result in increased soil erosion and siltation of rivers (Mason & MacDonald, 1986). The siltation of rivers may not actually deplete the otters’ food base, but curtails the availability of this food due to the increased difficulty in underwater foraging. Drainage of swamps for agricultural purposes, and increased use of pesticides may be a major threat to the long term survival of otter populations. Due to their position as tertiary consumers in aquatic ecosystems, they are vulnerable to bio-accumulation of pesticide residues from their prey species (Mason & MacDonald, 1986). Benthic macroinvertebrates like crayfish are especially prone to accumulation of heavy metal residues including lead and mercury. Otters are more directly threatened by the acidification of rivers and lakes because this interferes with calcium uptake by crustaceans. Crustaceans disappear at pH 5.3 because at this level, they cannot take in enough calcium to moult effectively (Moss, 1998). This would effectively eliminate *A. capensis* from that particular habitat.

1.2.1.5. **The Louisiana red swamp crayfish**

The crayfish is a decapod crustacean, indigenous to the south-eastern United States of America. The first introduction of crayfish into East Africa was in Uganda in 1960. *P. clarkii* was originally introduced to Kenya in 1966 when some individuals were transferred from Uganda Fisheries Department ponds at Kajansi near Entebbe into two dams located at Solai and Subukia in Nakuru District within the Kenyan Rift Valley (Foster & Harper, 2006).
Thereafter, it was introduced into the East basin of Lake Naivasha in 1970 (Lowery & Mendes, 1977). They spread rapidly and by 1977, they were prevalent throughout the Lake (Oluoch, 1990). Like most American crayfishes, *P. clarkii*, shows a high degree of biological plasticity, and they can establish themselves in nearly every type of freshwater habitat except glacial and thermal effluents (Thorp & Covich, 2001). They are extremely adaptable organisms capable of switching roles from herbivore/carnivore to scavenger/detritivore merely in response to food availability within the ecosystem (Thorp & Covich, 2001). The most commonly cited crayfish prey organisms are mollusks, insect larvae, worms, crustaceans and amphibian tadpoles (Holdich & Lowery, 1988). *P. clarkii* also produces the largest numbers of eggs recorded for crayfish species (Noblitt *et al.*, 1995). These capabilities have enabled this species to successfully invade freshwater ecosystems around the world and maintain large population densities despite fluctuations in food resources. *P. clarkii* is especially adapted to warm water habitats with continuous nutrient flow (Noblitt & Payne, 1995). In Lake Naivasha, crayfish have become the most important prey item for the largemouth bass and positive relationship was demonstrated between the commercial catch of bass in gill nets and the catch of crayfish from the trap fishery (Aloo, 1988, Hickley *et al.*, 1994). Crayfish activity diminishes rapidly as temperature drops below 14°C threshold (Covich, 1978), and this results in seasonal regulation of feeding and reproductive activity. In tropical countries such as Kenya, crayfish can, therefore, breed continuously in warm water habitats, but are excluded from the colder highland aquatic ecosystems.

1.2.2. Synergy between the Louisiana crayfish and the freshwater crab

The freshwater crab (*Potamonautes neumannii*) is a soft-shelled crab with an average adult weight of 10.3 grams (pers. obs.). It is abundant in Kenya’s highland aquatic
ecosystems, where it is sympatric with (*Potamonautes loveni*), another soft-shelled freshwater crab, which is orange in colour (Dobson, 2004). *P. neumannii* also occurs at lower altitude aquatic ecosystems in the rift valley, but in western Kenya, the Lake Victoria basin is occupied by (*Potamonautes niloticus*) (Dobson, 2004). The ability to reabsorb salt from urine and restrict water loss has enabled (*P. neumannii*) to be semi-terrestrial and forage on land (Morris & Van Aardt, 1998). It is, therefore, exploited as a food source by terrestrial predators such as the olive baboon (*Papio anubis*) in addition to the otters. Horns and Magnuson (1981) found that in Wisconsin, U.S.A.; (*P. clarkii*) consumes significant quantities of trout eggs, as well as those of other crustaceans. This may be one of the mechanisms by which (*P. clarkii*) has supplanted the indigenous crab (*P. neumannii*) in much of the lower Ewaso Ng’iro ecosystem. The crab and the crayfish are also direct competitors for food, with the crayfish prevailing due to its superior size and aggression. This has been demonstrated in the Lake Naivasha basin, where Foster and Harper (2006) hypothesized that *P. loveni* may have inhabited the lower stretches of these rivers prior to colonization by *P. clarkii*, but has since been predated or out-competed by the aggressive *P. clarkii*. It is also possible that *P. clarkii* has effectively wiped out downstream stocks of *P. loveni* by acting as a vector for a crustacean disease such as crayfish plague, *Aphanomyces astaci* (Foster & Harper, 2006).

Crayfish diet shifts during their development and is dominated by detritus in the adult stage (Holdich & Lowery, 1988). This brings them into direct competition with crabs for food and crayfish are also known to be predators of soft-shelled crustaceans in shared habitats (Thorp & Covich, 2001). Crayfish feed readily on macrophytes and they can reduce species richness and biomass of aquatic vegetation by selective grazing on plant species (Creed, 1994).
1.3 Rationale for the study

There have been many deliberate and accidental species invasions in Kenyan aquatic ecosystems in recent years, but the ecological effects in rivers have not been well-documented. Experimental aquaculture with the Louisiana red swamp crayfish in rivers has led to escapes and establishment of wild populations (Mikkola, 1978). These have replicated the detrimental effects of this species on Lake Naivasha as reported by Harper et al. (1990) and Njuguna (2005). The introduction of exotic species was identified as the most important threat to crab populations in East African rivers (Williams et al., 1964) and this forms the conceptual basis of this study. Kenya’s inland aquatic ecosystems have been heavily impacted by invasive species, but the nature and extent of this impact on the tertiary consumers in river ecosystems have not been properly assessed. Lotic habitats are fragile and easily changed by human activities including agriculture, clear-cutting of forests and species introductions (Giller & Malmqvist, 1998).

The Louisiana crayfish has been found to be responsible for the disappearance of water lilies and many species of snails in Eastern and Southern African wetlands (Howard & Matindi, 2003). It has also been found to be a threat to smaller species of fish like cichlids and killifish, with the potential to cause local extinctions (Howard & Matindi, 2003). It was, therefore, important to investigate whether this species has similarly impacted the Ewaso Ng’iro River ecosystem. In the lower Ewaso Ng’iro ecosystem, crayfish remains have recently been found to be a major component of otter faeces, suggesting that they have become an important food source for one of the most important predators in this ecosystem. Analysis of otter faeces over time reveals fluctuations in the availability of crayfish, which would also impact on other species that are prey or predators of crayfish. In the arid central Laikipia plateau, several small dams have been built by river users to provide water for
agricultural activities. These are ecologically important structures, particularly in shallow rivers like the Ewaso Ng’iro. It is important to assess the impacts of dams on species invasions since they are key to aquaculture, irrigation and recreation activities around the country.

This study on the territorial and food ecology of the African clawless otter will also increase knowledge about the species and threats facing it, which are unknown through much of its range.

1.4 Study Objectives

1.4.1 General Objective

To investigate the impact of the Louisiana red swamp crayfish (*P. clarkii*) on the diet and territorial behaviour of the African clawless otter (*A. capensis*) in the upper and lower parts of the Ewaso Ng’iro river.

1.4.2 Specific Objectives

a) To determine the distribution and abundance of the African clawless otter (*A. capensis*), the Louisiana crayfish (*P. clarkii*) and the native crab (*P. neumannii*) in the Ewaso Ng’iro ecosystem.

b) To investigate the interaction between the Louisiana red swamp crayfish and both the African clawless otter and the freshwater crab (*P. neumannii*).

c) To establish the effect of Louisiana crayfish distribution on the diet of the African clawless otter.

d) To establish the geographical extent of the presumed supplantation of the native freshwater crab (*Potamonautes neumannii*) by the Louisiana crayfish (*Procambarus clarkii*) in the Ewaso Ng’iro ecosystem.
1.4.3 Study Design

This study has been designed to take advantage of different ecological conditions occurring within the same river drainage and in relatively close geographical proximity, thus eliminating the need for any manipulation. In the absence of pre-invasion data, the effect of the Louisiana crayfish invasion is being assessed by using the Burguret study area as a model for ecological conditions before the crayfish invasion. The design of this study is, therefore, based on the following assumptions;

a) The African clawless otter and the freshwater crab, *P. neumannii* preceded the Louisiana crayfish in this ecosystem.

b) The freshwater crab, *P. neumannii* occurred throughout the Ewaso Ng’iro drainage prior to the Louisiana crayfish invasion, and has now been supplanted by the crayfish in the invaded areas.

c) Temperature is the only abiotic factor that is significantly different between the two study areas.

1.5 Study Hypotheses

a) There is no interaction between the Louisiana red swamp crayfish, the African clawless otter, and the indigenous freshwater crab in the Ewaso Ng’iro ecosystem.

b) The Louisiana crayfish invasion has not had any effect on the diet of the African clawless otter in the Ewaso Ng’iro ecosystem.

c) The Louisiana crayfish invasion has not had any effect on the territorial behaviour of the African clawless otter in the Ewaso Ng’iro ecosystem.
CHAPTER 2: MATERIALS AND METHODS

2.1 The Study Area

This study was carried out in the central part of Laikipia District and the northern part of Nyeri District in central Kenya, East Africa. It covered sections of the Ewaso Ng’iro River and two of its tributaries, the Burguret River and the Ewaso Narok River. The study areas were between 37°N0281424 East UTM9988012 North and 37°N0262755 East UTM0058753 North (Fig. 2). The Lower Ewaso Ng’iro study area comprised 20 kilometers of river frontage, whereas the Burguret study area included three kilometers of river. The Ewaso Ng’iro River flows from the Aberdares and Mt. Kenya through Laikipia and Samburu Districts of central Kenya, ending in the Lorian swamp. This study was based at the Mpala Research Centre in Laikipia. The property (2,200 ha) is situated northwest of Mt. Kenya, 50 km north of the Equator, and 50 km from Nanyuki town. The property is contiguous with the Mpala Ranch, a larger tract (20,000 ha) that is also available for wildlife and ecosystems research. The Laikipia area is dissected by the Ewaso Ng’iro River and its tributaries which arise in the Aberdare Mountains and Mount Kenya. This river system is an important component of the Laikipia and Samburu ecosystems because it is a semi-arid area receiving an average of 600 mm of rainfall per annum (Paton & Ogada, 2001). It is the only permanent water source for numerous herds of livestock reared by ranchers and pastoralists in the area as well as a large wildlife population, particularly in the Samburu National Reserve. The river water levels fluctuate greatly between seasons from a minimum of 0.33 meters deep and a maximum of 3.5 meters deep measured at a gauge mounted at Mpala Research Centre.
Figure 2. Map of Laikipia Showing the two study areas.
Over 1000 plant species occur within the study area. The vegetation is characteristic of semi-arid African savannahs, predominantly grassy savannah bushland, with patches of woodland and open grassland. Dominant trees include species in the genera *Acacia* (Mimosaceae), *Euphorbia* (Euphorbiaceae), *Balanites* (Balanitaceae), and *Boscia* (Capparaceae). The southern (Burguret river) end of the study area is at the edge of Mt Kenya forest, dominated by African olive *Olea africana*, *Podocarpus latifolia* and Cedar *Juniperus procera*. It is also home to several wild mammal species, including elephants, leopard, olive baboon, colobus monkey, bushbuck, and sunni. It has higher rainfall (average 800mm per annum) than the lower Ewaso Ng’iro study area and the river level varied between a maximum of 35 cm and 8cm depth at the gauge during the study period.

Cattle, camels, sheep and goats are reared in the northern part of the study area, but the region also hosts an intact savannah mammal community, including Kenya's second largest elephant population. More than 75 mammal species and at least 400 bird species are found in this area including elephant, eland, zebra, oryx, reticulated giraffe, waterbuck, impala, Grant's gazelle, Jackson's hartebeest, bushbuck, lions, leopards, cheetahs, spotted hyenas, black-backed jackals, aardwolves and bat-eared foxes.

The lower Ewaso Ng’iro study area consisted of 20 km of river frontage whereas the Burguret study area had 3 km of river frontage. The sizes and locations of these study areas were determined by accessibility and residents/landowners permitting the team to carry out the surveys.

### 2.2 Methods

Crayfish and crabs were sampled using funnel-mouth traps already used in the preliminary sampling exercise. These were made using 1.875 centimeter size wire mesh reinforced with binding wire. They were then weighted with stones, placed on the bottom of the river,
baired with meat and secured to the river bank using coloured nylon string. Traps were checked, emptied, and re-baited every 24 hours. Sites were located every 1 km within the Ewaso Ng’iro, Ewaso Narok, and Burguret river study sites.

Crayfish caught in the funnel-mouthed traps were weighed and measured to establish the age distribution. Weight of the crayfish and diameter of their antennules and antennule bases were also noted in order to derive a mathematical relationship between the two variables. Antennules were chosen for measurement because being situated on the cephalothorax, they are always eaten by the otter (unlike claws or legs, which are sometimes discarded) and are usually retrieved intact from otter faeces. The fact that there are only 2 antennules per crayfish, allows for the deduction of numbers eaten to a high degree of accuracy. The antennule bases were measured using vernier calipers. The composition, abundance, and frequency of the faecal samples in the study area were an additional indicator of fluctuations in the distribution of the otters and their prey.

The northern study area was divided into three ‘blocks’ based on different river sources.

a) The Ewaso Ng’iro River upstream of the junction with the Nanyuki river.

b) The Nanyuki River and the Ewaso Ng’iro downstream from the junction of the two rivers.

c) The Ewaso Narok River (a tributary of the Ewaso Ng’iro).

The divisions upstream and downstream of the junction with the Nanyuki River were made in order to detect abiotic or biotic influences of the urban use (Nanyuki town) on the river. The Ewaso Narok River flows from a different source (Ewaso Narok swamp) and seasonal variation differs in rhythm from that of the main Ewaso Ng’iro River.

Otter territorial behaviour in these blocks was compared to the southern (Burguret River) study area, which was not divided into blocks, because it did not include any junctions.
Otter population densities were estimated by effects (Caughley, 1977), which involves clearing otter faecal pellets from the study area and analyzing the faeces deposition rates thereafter. In the absence of capture data, frequency of faecal deposits was also used to deduce temporal distribution of otters within the study area. Water depth and temperature were noted whenever spraints were collected in order to examine the possible effects of abiotic factors on otter and crustacean distribution. The Ewaso Ng’iro and Burguret water levels were measured at permanent river gauges set up by the Ewaso Ng’iro North Development Authority (ENNDA). The distribution of prey species was inferred from the composition and locations of the spraints collected. Therefore, otter habitat sites were classified according to the composition and frequency of pellets collected there. These were then analyzed against river water levels to identify the more important abiotic factor. This is a modification of the ordination method (Begon et. al., 1996). In its original form, this method was found inappropriate for assessment of abiotic factors over time in a flowing aquatic habitat because it assigned values of abiotic variables such as pH to a particular point in a flowing liquid medium.

For the assessment of population density, more emphasis was placed on spraint collection and camera trap photography as indicators than trapping and marking of otters. This is because repeated trapping at latrine sites caused the otters to abandon them, thus jeopardizing a valuable data source for this study. The data obtained from the various observation methods was recorded and presented in graphical format to show the biotic changes through the study area that may be influenced by geographical features particularly deep water pools and river junctions.

Otter distribution along the same stretch of the Ewaso Ng’iro was initially investigated by direct observation (between 06.00h & 10.00h, and between 16.00h & 19.00h when the
animals appeared to be most active and could be observed through binoculars) and by finding faecal deposits (spraints). Sightings of otters and locations of spraints were recorded using a Global Positioning System (GPS). Spraints were collected by manually searching both river banks and taken to the laboratory where they were dried, sorted and their contents identified. Again using antennule base size, the size distribution of prey were compared to the size distribution obtained from trapping, to determine if otters selectively took different sizes of prey. A mathematical relationship between the antennule base size and overall weight of live caught crayfish was also used to deduce the mass of crayfish being taken by otters on a daily basis.

Otters were live-trapped in Tomahawk single-door, rigid live traps baited with fish (Wilson et. al., 1996), and otter spraints from other territories (Michael Somers, pers. comm), marked and released. Trapped animals were anaesthetized using a pole syringe, using etorphine hydrochloride (M99). This is an oripavine derivative considered to be one of the most versatile agents available today for the chemical immobilization of mammals (Day et. al., 1980). The clinical effects of M99 can be reversed rapidly by employing any one of four specific antagonists (Diprenorphine, Cyprenorphine, Nalorphine hydrobromide, and Naloxone HCl) to produce rapid reversal of the clinical immobilizing effects.

Diprenorphine was used in this study. The anaesthetized animal was then marked and released. Two marks were made on each animal, one on the back of the head and one at the base of the tail. These were the most visible sites when an otter was running or swimming away from the observer. The two spots were first washed with ethyl acetate to remove the natural oils from the fur, then the marks were made using ‘ABRO’® brand automotive spray paint. This resulted in a mark lasting 8 months. This method was preferable to plastic rings and ear tags, which otters could easily remove with their fingers.
Observations were made of other animals and birds foraging in the river in order to identify those that could be competing for the same prey base exploited by the otters. These competitor species were identified either directly, or from faecal pellets and prey remains discarded near nests and roosts.

The motion sensor camera (Cam Trakker) was moved from site to site in order to confirm and extend the estimates of otter home range sizes obtained from observation and trapping. The Cam Trakker is a fully automated 35mm camera combined with a passive infra red motion detector, powered by 4 alkaline batteries. This method, however, was discontinued due to insecurity (theft of cameras). The final and most reliable estimates of size and location of otter territories (in terms of length of river frontage) was by the ‘scats and glue’ method (Ogada, 2004). This involved placing spraints on rocks along the river at 100-meter intervals and these were moved another 100 meters every 24 hours. At every point, the spraint was placed on a rock and secured with a small amount of glue. Cyanoacrylate (‘super glue’ brand) was used because it dried quickly and produced no discernible odour after 15 seconds. The glue was to prevent the experimental spraint from being blown off by the wind or washed off by rain. Using a permanent marker, a small blue mark was made on the spraint to facilitate its positive identification the following day. Within the initial territory, the experimental spraint did not elicit any response from the resident otters. However, when the spraint reached another territory, the resident otters responded by removing it and replacing it with a fresh one. The fresh spraint was then taken and the process repeated in the opposite direction until a similar response was elicited from the original group. The GPS position of a point midway between the two response points was recorded and this was taken to be the end of the territory. Otters are generally low-profile animals, rarely seen in the wild, even in areas of relatively high density. The standard
method for assessing population density and distribution is therefore by surveying for spraints (faeces) and footprints (Mason & MacDonald, 1986). Spraints of *A. capensis* were found on rocks, fallen trees, islets, and spits of land protruding into the river. Footprints were found on sandbanks and muddy riverbanks in the study area. This was consistent with the habits of the European otter (*Lutra lutra*), on which these survey methods were developed (MacDonald *et. al.*, 1978). However, there is a great difference in the numbers and diversity of wild and domestic animals visiting African and European riverbanks. Otter footprints in this particular study area were frequently obscured by the prints of baboons (*Papio anubis*), monitor lizards (*Varanus niloticus*), hippos (*Hippopotamus amphibius*), and livestock (sheep, goats and cattle) all of which frequented the sandbanks and muddy banks used by the otters. Population parameters for this particular study were therefore estimated by records of spraints alone.

Competition between crabs and crayfish was simulated by placing 10 crabs and 10 crayfish in a 50 liter perspex tank. They were fed with ox heart cut into 1cm cubes and water was changed every 12 hours. Observations were made every 12 hours to note how many crabs and crayfish were alive. This was done in an open tank and repeated with rocks in the tank to simulate natural shelter used by crabs. The experiment consisted of a total of 10 observations, made over a total of 120 hours.

For purposes of assessing feeding depths of herons, which were potential competitors for crayfish various dimensions of the species found in the Laikipia plateau were measured. The measurements were taken from specimens preserved at the National Museums of Kenya Ornithology Department using a metric tape measure. These specimens were measured in order to determine which species would be the most important influence on the availability of crayfish to otters at different river levels.
For assessment of profitability of crustacean prey, live specimens were randomly selected (every 20\textsuperscript{th} specimen caught in the sampling traps), weighed and their weights recorded. They were then sectioned and boiled to facilitate the manual removal of soft tissues from the skeletal parts. The skeletal remains were then dried and their dry weights recorded.

### 2.3 Data Analysis

a) Weights of crayfish caught in the wire mesh traps were regressed against the diameters of their antennule bases (Plate.4) to establish a linear relationship:

$$ W = (-x + yD) $$

-Where ‘$W$’ is weight, ‘$D$’ is antennule diameter, and $x$ and $y$ are the respective axes.

This was then used to deduce the amount (weight) of crayfish being consumed by otters from various points in the study area, as well as the otters’ preferred prey size. This method was adapted from that used by Kruuk & Goudswaard (1990) to deduce otter prey (fish) sizes by measuring the diameter of fish eye-lenses retrieved from faecal pellets.

b) Density of otter spraints (# spraints per unit length of river) within seasons was regressed against proportion of crayfish (by mass) in the spraints to determine whether availability of crayfish is influencing the otters’ use of the habitat. Seasons, in this context, were defined by river levels, rather than precipitation within the study area. This was used to illustrate the interaction between the otters and the crayfish.

c) Temporal trends in water temperature, territorial marking, and otter density were compared between the two study areas by ‘t’ test (Huntsberger, 1972)
d) Temporal and spatial fluctuations in otter faecal pellet composition was teased out of bivariate scattergrams of the same using a LOWESS curve (Cleveland, 1981).

e) Characterization of otter habitats was done by graphically plotting the proportions of crustacean prey in otter faecal pellets at different river levels against the GPS locations at which the pellets were collected. Crustacean prey is the primary food source for African clawless otters (Rowe-Rowe, 1977). However, the proportion of crustacean remains in otter faecal pellets was found to fluctuate with river water levels within the study area. Otter habitat quality was, therefore, assessed based on the stability of crayfish content in the faecal pellets collected at a location across different river levels. The effect of depth on otter scat composition over time revealed the impacts of dam construction on the diet and habitat use by otters.

f) All statistical analyses were done using 'STATVIEW' program (SAS, 1998).

g) Population density of otters was estimated using scat counts over time (Caughley, 1977). The data was then analyzed using the transect method;

\[
D = \frac{nT}{LW}
\]

Where; \( nT \) is number seen on the transect, \( L \) is length of the transect, and \( W \) is width of the transect (Caughley, 1977). For purposes of this study, the formula was modified to;

\[
D = \frac{nT}{L}
\]

This was done because the otter habitats in this study area (rivers) were linear.

Otter population densities in this study area are, therefore, expressed in terms of animals.
per unit length of river. For the purposes of analysis, each survey for scats was treated as a sample count and means were calculated for each month.

Scats of other terrestrial and avian predators observed foraging at the rivers were examined for evidence of crustacean remains. This was done in order to identify the otters' potential competitors.
Plate 4. The position of the antennule base on the Louisiana crayfish
CHAPTER 3: RESULTS

3.1 Weight distribution of crayfish in the Ewaso Ng’iro study area.

Trapping in the lower Ewaso Ng’iro study area yielded a total catch of 406 crayfish in 6 months. It was discontinued thereafter to avoid compromising the assessment of otter dietary content in the study area. The mean weight of Ewaso Ng’iro crayfish was found to be 31.857 grams (SD=17.504) and the weights of sampled individuals were distributed between 5-80 grams (Fig.3) with the majority falling between 20-40 grams weight. The crayfish weights were regressed against the diameters of their antennule bases to yield a mathematical relationship as follows; \( y = -36.891 + 58.87 \times \); \( R^2 = .902 \).

![Figure 3. Weight distribution of trap sampled crayfish in the Ewaso Ng’iro study area](image)

Where ‘\(y\)’ is the weight of the crayfish and ‘\(x\)’ is the diameter (in millimeters) of the antennule. This was then used to calculate crayfish intake by the otters in subsequent
analyses. The diameter was the preferred dimension because most antennules retrieved from otter faecal pellets were broken along their length during the process of mastication.

The weights of crayfish eaten by otters were calculated from antennules found in faeces using the above formula. These were also normally distributed with the majority being between 13-21 grams (Fig. 4).

![Figure 4. Weight distribution of crayfish eaten by otters in the Ewaso Ng’iro study area.](image)

3.2 Otter territories in the study area

Lengths of otter territories in the two study areas were compared by ‘t’ test and those in the lower Ewaso Ng’iro study area found to be significantly larger than those in the Burguret study area. There was a mean difference of 2633.33 meters ($t = -5.019, p<0.05, df=2$) between the sizes of otter territories in the two study areas. This was based on results obtained using the ‘scats and glue’ method (Ogada, 2004). There were three territories
identified in the lower Ewaso Ng’iro study area and four identified in the Burguret study area (Fig. 5).

The numbers of otter territories, therefore, indicate that the density of otters is 8.9 times higher in the Burguret area, assuming similar numbers of individual otters in each territory. Territorial behaviour by otters consisted of aggregation of faecal pellets at holts and this varied on a monthly basis. There was a 30.158% mean difference between the intensity of territorial marking in the two study areas with the Burguret area being markedly higher (t=5.030, p<0.0004, n=2) (Fig. 6). There was also a significantly higher monthly variation in the intensity of territorial marking by otters in the Ewaso Ng’iro study area (mean diff. 16.255%, ‘t’=2.767, p<0.05, df=10).

3.3 Dietary trends of otters in the study area

Crayfish were the most important food item for otters in the lower Ewaso Ng’iro. This was indicated by a mean proportion of 60% crayfish remains in all otter faecal pellets collected in the area during the 2 year study period. This was followed by fish, ‘others’ (insects, lizards and ungulate dung) and crab remains respectively (Fig. 7). Proportions of both fish and crayfish remains in faecal pellets were found to vary from 0-100% during the course of the study.
Figure 5. Map of the study area showing otter territories (black boxes) and the 14 degree centigrade threshold.
The calculated weight of crayfish eaten per faecal pellet was significantly correlated
(corr=0.325, \( p<0.0001 \), \( n=285 \)) to the river water level on the respective collection date.

The otter scats collected in the Burguret study area consisted almost entirely of crab remains
(Fig.8).

![Graph showing percentages of aggregated faecal pellets and mean monthly pellet collections in two study areas (Burguret and Ewaso Ng'iro) from January to December (2003-2004).](image-url)

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Figure 6. Percentages of aggregated faecal pellets and mean monthly pellet collections
and in the two study areas (2003-2004).
3.4 Effects of river water level on faecal pellet composition and collections.

The Ewaso Ng’iro River level varied between a maximum of 350 centimeters and a minimum of 32 centimeters. The Burguret River level varied between a maximum of 35 centimeters and a minimum of 8 centimeters at the gauge. Analysis of the lower Ewaso Ng’iro river levels when pellets were collected gave a negative
Figure 8. Burguret otter diet composition (2003-2004)

correlation (Corr.= -0.077, 'z'= -1.820, \( p > 0.05, n=564 \)) but this was not statistically significant. However, a histogram of the same (Fig. 9) revealed a threshold at 38cm river level beyond which there was a sharp rise in numbers of pellets collected. There was no significant variation in the content of faecal pellets collected in the Burguret study area, with the minimum crab content being 97.25% by weight. There was also no relationship between the river water level and the number of faecal pellets collected in the Burguret study area (Corr= -0.508, 'z'= -1.253, \( p > 0.05, n=487 \)).
Biomass of crayfish consumed by otters in the Ewaso Ng’iro study area was calculated from the numbers and base widths of antennules retrieved from faecal samples, using the equation in section 3.1. There was a significant positive correlation (corr.=0.325, ‘z’=5.665, p<0.0001, n=285) between the crayfish biomass removed from the river per faecal pellet and the river level. This correlation was calculated using only the faecal pellets which contained intact crayfish antennules. The trend is strong unto the depth of 175 cm, beyond which it becomes difficult for otters to forage in the benthic region due to the strong current.

Figure 9. Faecal pellet collections at different river levels in the Ewaso Ng’iro study area.
The relationship between otter diet and river level is also illustrated using a bivariate scattergram of crayfish percentage in faecal pellets and the river level on their respective collection dates. A lowess curve (Cleveland, 1981) at tension value of 66 showed parallel trends in the 2 variables measured over the study period (Fig. 10).

Figure 10. Crayfish percentages per faecal pellet at different river levels in the Ewaso Ng’iro study area.

There was a rapid oscillation in the percentage of crayfish remains in otter faecal pellets from the Ewaso Ng’iro study area. This is illustrated using a histogram showing the frequencies of various faecal pellet compositions. The highest frequency recorded was that
of faecal pellets composed of 100% crayfish remains followed by faecal pellets with 0% crayfish content.

Figure 11. Relative frequencies of crayfish content in otter faecal pellets from the Ewaso Ng’iro study area.

3.5 The dimensions of heron species found in the study area

There were 3 species of herons observed foraging on crustacean prey in the Ewaso Ng’iro study area. These were the goliath heron (*Ardea goliath*), the grey heron (*Ardea cinerea*) and the black-headed heron (*Ardea melanocephala*). They feed in shallow water, not venturing to depths beyond the lower limit of feathering on their legs. The measurements
for these species were taken from specimens kept in the reference collection at the National Museums of Kenya.

Figure 12. Dimensions of black-headed heron specimens

Figure 13. Dimensions of grey heron specimens
Figure 14. Dimensions of goliath heron specimens

3.6 Assessment of otter habitat quality in the study area

The observations were placed on either side of the 38cm river level threshold based on the collection frequencies presented in Figure 9. For the purposes of these graphs, only UTM locations were used because the rivers being surveyed generally followed a Northward trend, so there was no danger of location overlap. For the Lower Ewaso Ng’iro study area, there were four high quality otter habitats, which yielded high crayfish content pellets even below the 38cm threshold. These locations were then identified from the faecal pellet collection records (Fig. 15). ‘A’ was a natural pool at Surungai near the southernmost end of the study area. B and C were man-made water reservoirs (dams) on Jessel and Mpala ranches respectively. D was a natural pool at the confluence of the Ewaso Ng’iro and Ewaso Narok rivers.
Figure 15. Crustacean prey availability in the lower Ewaso Ng’iro study area.

Analysis of the crayfish content in the lower Ewaso Ng’iro faecal pellets using a lowess curve (tension=66) revealed a net decline in crustacean prey availability as one moves downstream to the North (Fig. 15). At the confluence of the Ewaso Narok and Ewaso Ng’iro rivers, the availability of crayfish had declined to the level where it was no longer influenced by the river water level. A similar analysis was done on the faecal pellets collected from the Burguret study area (Fig. 16). This revealed a high density of otter holts across the study area, and no significant difference in crustacean prey (crab) availability across the study area. There was also no detectable change in the crab content of faecal pellets collected at river levels above 20 cm and below 20 cm.
3.7 Abundance of crustacean prey in the study area

There were large proportions of crab and crayfish in otter faeces from the Ewaso Ng’iro and Burguret study areas respectively. Abundance of crayfish and crab in the two study areas were measured by numbers of individuals caught per trap night measured on a weekly basis. The numbers of crayfish caught per trap night diminished at a rate of
6% per month over the 18-month trap sampling period and reached a low of zero in April 2004 (Fig.17). Analysis of contents of otter faecal pellets from the two study areas over the same period by unpaired ‘t’ test shows that otters in the Ewaso Ng’iro study area were consuming a significantly higher ('t' value = 15.158, df = 1007, p < 0.0001) proportion of fish than those in the Burguret study area. This corroborates the decline in trap sampling yields of crayfish in the Ewaso Ng’iro study area.

3.8 Otter population density in the study area

The average otter population density in the Burguret study area over a period of one year was 6.951 otters per Km. of river. The average otter population density in the Ewaso
Ng’iro study area over 21 months was 1.225 otters per Km. of river. A comparison of means in the two study areas from January to December 2004 was done by ‘t’ test and the Burguret density was found to be significantly (mean diff. = 5.198, t'value = 10.958, df = 11, p<0.0001) higher than that of the Ewaso Ng’iro study area (Fig. 18). An analysis of trends showed a net rise of 5.7% in the Burguret study area and an 80.769% decline in the Ewaso Ng’iro study area during the study period.

![Figure 18. Monthly mean otter population densities in the 2 study areas.](image)

The ‘x’ intercept calculated from this trend over time indicates that if the current rate of decline in otter population is maintained, otters will be locally extinct in the Ewaso Ng’iro study area 34 months after the beginning of this study, i.e. by October 2005. This follows 17 months after the trap sampling yields have declined to zero level (Fig.19). The otter
population trend was correlated to the crayfish abundance in the Ewaso Ng'iro ($corr=0.402, \ 'z'=1.652, df=18, p>0.05$) but this was not statistically significant.

3.9 Productivity of the two study areas in terms of otter nutrition.

Assessment of the otters' functional responses to the food items available in the two study areas was based on the availability and nutritional quality of crabs and crayfish. The relative weight of prey species remains in otter spraints was first determined. For the crayfish

![Graph showing otter density and crayfish abundance over time.](image)

**Figure 19.** Comparison of Ewaso Ng’iro otter population trend and crayfish trap sampling yield.
prey, this was the weight of the exoskeleton relative to the live weight, and for osteichthyes (bony fish) this was the weight of the endoskeleton relative to the live weight. Scales were not considered in this calculation to eliminate the error from species like catfish, which do not have scales. The protein content per unit weight of the crabs was significantly higher \((\text{mean diff} = 7.449, \text{df} = 19, t' = 17.281, p < 0.0001)\) than that of crayfish. However, crayfish had a higher average live weight than the crabs (Fig. 20). The bony fish had the highest protein content per unit body weight, although they are not a major food source for the otters, which live almost entirely on crustacean prey (Rowe-Rowe 1977a, 1977b) due to their lack of claws that makes it difficult to capture fish. Over two years, bony fish remains comprised less than 1% of the faecal material in samples collected in the Burguret study area. The relatively high proportion (36%) of fish in otter faeces collected from the Ewaso Ng’iro study area is more an indication of food stress, rather than a switch to a new food source. Between the two crustacean prey species, the freshwater crab \(P. neumannii\) was found to be the more profitable to the otters per unit weight eaten due to their relatively low proportion of indigestible (exoskeletal) material per unit body weight.
Figure 20. Live weights and protein contents of crustacean prey species in the two study areas.

The numbers of crustacean prey eaten per unit time were calculated. For crayfish, this was done using the number of antennules retrieved from faecal samples over time.

_Potamonautes neumannii_ are soft-shelled crabs, which were easily crushed by the otters. Consequently, their remains in otter faeces consisted of very small fragments from which various crab parts were not easily distinguishable. The otters’ estimated crab consumption rate in the Burguret study area was therefore given by the following formulae;

\[
\text{Crabs eaten (Ce)} = \frac{To \{ (P/E) + 1 \}}{W}
\]

Where; P is the mean protein content per crab in _P. neumannii_, E is the mean exoskeleton content in the same, W is the average weight (gm) of _P. neumannii_ specimens, and CW is
the total weight of crab remains in otter faeces from the study area. The estimated daily intake of crabs per otter in the Burguret study area is therefore given by:

\[
\frac{(Ce/Op)}{T}
\]

Where; Ce is number of crabs eaten in the study area, Op is mean otter population density in the study area and T is time in days. The number of crabs eaten estimated from the faecal pellets collected in the study area (Ce) was;

\[
\frac{CW(P/E)+1}{W} = \frac{10656}{10.3} = 21724.2\{(\frac{80.206}{19.794})+1\} = 10656 \text{ crabs}
\]

The estimated number consumed by each otter per day was therefore;

\[
\frac{(Ce/Op)}{T} = \frac{10656/11.9938}{365} = 2.4341 \text{ crabs per day.}
\]

Further calculation revealed the amount of crustacean protein obtained daily by otters in the Burguret study area to be;

\[
(2.4341 \times 10.3) \times 80.206 = 20.1086 \text{ grams per day}
\]

The above figures however, are likely to be underestimates because in the months of April, May, and November, there was a 43.2% mean reduction in faecal pellets collected. This was due to heavy rains and flash flooding which washed faecal pellets off the territorial marking spots.

In the Ewaso Ng’iro study area, a total off take of 840 crayfish during the study period was estimated from remains found in the otter faecal samples. The estimated consumption rate for each otter was;
The total weight of crayfish off take estimated from remains in otter faecal samples was 14.923 kg. This gives a mean weight of 17.765 grams per crayfish.

The rate of crustacean protein intake for otters in the Ewaso Ng’iro study area was given by:

\[ \frac{Cd(Cw \times Cp)}{100 \times Op} \]

Where; Cd is daily crayfish off take, Cw is mean calculated crayfish weight, Cp is the protein content per crayfish, and Op is the otter population in the Ewaso Ng’iro study area.

\[ \frac{2 \times 17.765 \times 72.757}{100 \times (1.224638 \times 23)} = 0.91777 \text{ grams per day} \]

The crustacean prey intakes calculated for the two study areas are derived from materials retrieved from faecal pellets. The deductions are, therefore, subject to two major sources of error. Firstly, there is the loss of faecal pellets due to being washed away from latrine spots by heavy rain or flash floods. Secondly, there is the possibility of random faecal deposition by otters away from latrine spots and the consequent difficulty in locating them.

The final figures for crustacean prey intake are therefore likely to be underestimations of the otters’ true food intake in nature. However, with the assumption that both study areas were subject to the same sources of error, these figures are an accurate indication of the relative availability of crustacean food to the otters in the two study areas.
3.10 Brown trout as potential competitors to otters in Burguret River

Brown trout (Salmo trutta) are an invasive species present in the Burguret river and crab forms a significant portion of their diet (Fig. 21). This fish was been introduced by sport fishermen stocking the upper reaches of the river and lakes in the Mt. Kenya moorlands. Some trout also escape from the Tam Trout fish farm whenever the tanks overflow due to heavy rains. This fish farm is situated at the Northern end of the Burguret study area. They rear brown trout for sale as food, and as fingerlings for stocking sport fishing venues. The stomach contents of 51 individuals caught by local fishermen were examined and found to contain 61% (by weight) remains of juvenile crabs. This makes them potentially important competitors for the otters’ crab prey base in the Burguret river study area.

Figure 21. Stomach contents of Burguret river trout (July-December 2004).
3.11 Variations in Ewaso Ng’iro river levels and otter territorial behaviour

The degree of otter territorial behaviour was inferred from the proportion of aggregated faecal pellets (Fig.22).

![Graph showing the relationship between mean monthly river level and mean monthly percentage of aggregated faecal pellets.](image)

**Figure 22. Effect of Ewaso Ng’iro water level on faecal pellet aggregation**

The mean monthly proportion of aggregated faecal pellets was plotted against the corresponding mean monthly river level in a bivariate scattergram with histograms. The histograms mirrored each other, i.e. the aggregation of faecal pellets declined with increasing water levels above 39 cm. The histogram also showed that there was no aggregation below 35 cm water level.
3.12 Variation of daily maximum water temperatures in the study area

The mean daily maximum water temperature in the lower Ewaso Ng’iro study area during the study period was 19.748 degrees Celsius. This was significantly (mean diff=7.177, ‘t’ value=65.447, df=400, p<0.0001) higher than that of the Burguret study area, which was 12.643 °C (Fig 23)

![Graph showing water temperature variations in the study area (2003-2004)](image)

Figure 23. Water temperature variations in the study area (2003-2004)

3.13 Competition between captive crabs and crayfish.

Two competition experiments were set up by placing 10 crabs and 10 crayfish per tank in two tanks. Observations over a period of 120 hours showed that crayfish would always prevail over crabs in direct fights because the crayfish had much larger claws. Crabs would
therefore take refuge from the crayfish by climbing out onto the rocks provided in one of the experiments. Consequently, the percentage of crabs killed by crayfish in the open tank per unit time was significantly (mean diff=56, t-value=9.058, df=9, p<0.0001) higher than that of the tank with rocks (Fig. 24).

![Figure 24. Crab mortality rates due to competition with crayfish.](image.png)
The above experiment demonstrated that direct competition and predation is a key component of the mechanism by which *P. clarkii* has supplanted *P. neumannii* in the Lower Ewaso Ng’iro river. It also shows that the ability of crabs to hide under rocks only provides them with a temporary refuge from this threat. The only escape for them in the field would be to leave the water, thus exposing themselves to terrestrial and avian predators.

### 3.14 Distribution of otter faecal pellets in the Ewaso Ng’iro study area

GPS locations of faecal pellets collected in the Ewaso Ng’iro study area were recorded and those within radii of 20 meters or less were combined on the map. The locations were mapped every 8 months (Figs. 25, 26, 27) during the study period to give 3 maps graphically documenting trends in otter distribution in the area.

There was a 39.26% net decline in numbers of faecal pellets collected between the first and third 8-month time blocks. The maps also show changes in the otters’ use of the habitat and territorial marking as reflected by the distribution of the faecal pellets. Single (non-aggregated) scats were not included in the above maps. The black circles illustrate the numbers of scats collected at the indicated locations.
Figure 25. Ewaso Ng'iro faecal pellet collections January-August 2003

Figure 26. Ewaso Ng'iro faecal pellet collections September 2003-April 2004

Figure 27. Ewaso Ng'iro faecal pellet collections May-December 2004
3.15 Stomach content of monitor lizards in the Ewaso Ng’iro study area

A total of 21 monitor lizards were caught in traps during the study period. The ones caught in otter traps (9 individuals) were released, but the ones caught and drowned in crayfish sampling traps (12 individuals) were dissected. The stomach contents were dried, separated and identified. They were then weighed in the lab and proportions were assigned by weight. Crayfish formed the largest single portion of the diet (Fig. 28). This indicates that monitor lizards could become important competitors for the diminishing crayfish prey base.

Figure 28. Diet composition of Ewaso Ng’iro monitor lizards
3.16 Species richness in the lower Ewaso Ng’iro ecosystem

Records taken at the beginning (Table 1) and the end (Table 2) of this study shows a reduction of 75% in the absolute number of aquatic species caught in sampling traps in the lower Ewaso Ng’iro during the study period. There was no reduction in the number of species caught in sampling traps in the Burguret river during the same period.

Table 1. Total number of aquatic species captured in sampling traps, February 2003

<table>
<thead>
<tr>
<th>Class</th>
<th>Common Name</th>
<th>Species</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Osteichthyes</td>
<td>Tilapia</td>
<td>Oreochromis niloticus</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oreochromis baringoensis</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Barbel</td>
<td>Barbus paludinosus</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barbus intermedius</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barbus leumayeri</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Labeo cylindricus</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Catfish</td>
<td>Clarias gariepinus</td>
<td>1</td>
</tr>
<tr>
<td>Amphibia</td>
<td>Frog</td>
<td>Rana angolensis</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Clawed frog</td>
<td>Xenopus laevis laevis</td>
<td>9</td>
</tr>
<tr>
<td>Crustacea</td>
<td>Freshwater crab</td>
<td>Potamonautes neumannii</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Crayfish</td>
<td>Procamburus clarkii</td>
<td>81</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
<td>12</td>
</tr>
</tbody>
</table>
Table 2. Total number of aquatic species captured in sampling traps November, 2004

<table>
<thead>
<tr>
<th>Class</th>
<th>Common Name</th>
<th>Species</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Osteichthyes</td>
<td>Barbels</td>
<td>Barbus intermedius</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barbus leumayeri</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barbus paludinosus</td>
<td>6</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td></td>
<td>38</td>
</tr>
</tbody>
</table>

The territorial behaviour of otters indicates the concentration of crayfish in deep water pools during the dry seasons. This concentration is likely to impact negatively on the other aquatic fauna making use of these deep water refuges, since crayfish consume significant quantities of fish, crustacean and frog eggs.

The diversity of sample catches was analyzed using the Shannon-Wiener index. The sample catch from February 2003 gave an $H'$ value of 1.225, while the sample catch from November 2004 gave an $H'$ value of 0.276, showing a reduction of 63%.
CHAPTER 4: DISCUSSION

4.1 Food ecology of the African clawless otter in the Ewaso Ng’iro ecosystem

Under the best of circumstances, the African clawless otter, in much of its range, lives at the edge of what is energetically sustainable. It is rare and difficult for any predator to survive on a prey species that weighs an average 0.07% of its own body weight. The otter must, therefore, spend much of its waking hours foraging. It also follows that the prey species must be very abundant and easily available. Using lions as an example, Schaller (1972) found that predators need to eat 24.96 times their weight in prey per annum. However, the energy requirement per unit body weight of lions, which run after their prey is 1.4 times higher than that of otters, which swim after their prey (Eckert et al., 1988). This suggests that an 18kg otter would therefore need to consume:

\[ 18 \times (24.96 \div 1.4) = 18 \times 17.82857143 = 320.9 \text{ kg of prey per annum.} \]

Otters eat crabs by choice (Rowe-Rowe, 1977b) and the average weight of \( P. \text{neumannii} \) specimens from the Burguret river is 10.3 grams. Therefore, to achieve this target from crustacean prey alone (which would be the ideal situation), the otter would need to eat a total of;

\[ 320900 \div 10.3 = 31155.33981 \text{ (} P. \text{neumannii} \text{) crabs per annum or 85.357 crabs per day.} \]

It, therefore, follows that otters will be more successful in habitats where they live on larger crustacean prey species. This is because they will be able to meet their daily requirement with lower expenditure of energy. For example, otters living in Maji ya Chai River in Tanzania prey on \( P. \text{phaenoticus} \) crabs that, on average, weigh 20 grams. This is approximately twice the average weight of \( P. \text{neumannii} \) specimens from the Burguret River. These otters would, therefore, need to eat approximately;

\[ 85.357 \div 2 = 42.6785 \text{ crabs daily.} \]
The functional response to a larger prey species would be beneficial to the otters. The handling time for a large crab does not differ significantly from the handling time for a small crab. The search time for a larger prey species may be reduced in a case where the otter is foraging by touch in turbid water. Otters living on the rocky coastlines of South Africa are particularly successful due to the nature of their main prey species: the red rock crab (*Plagusia chabrus*), octopus (*Octopus granulatus*) and suckerfish (*Chorisisomus dentex*). The red rock crab and octopus are easily visible and highly profitable respectively. Octopus, on average, weighs 138.2 grams (Van der Zee, 1981) and is easy to grasp because of the suckers on its tentacles. The red rock crabs (*Plagusia chabrus*) weigh on average 12.7 grams (Van der Zee, 1981) and hide under rocks, but the otters easily reach them using their well-developed digits. The suckerfish is particularly ideal, because its profitability (average weight 17.29g) is enhanced by its sedentary status as it attaches itself to rocks.

These circumstances provide for otter populations that are highly visible because they spend less time in the water foraging, hence the ease of direct observation detailed in the study done by Somers (2000).

Given its diet restrictions, *Aonyx capensis* would be unlikely to live at high densities even in ideal conditions. They are, therefore, highly vulnerable to disruptions of their food base or disturbances of their habitat. The World Conservation Union (IUCN) does not list the African clawless otter as vulnerable or endangered, but this is more due to lack of data than stability of populations. Its status should be listed as vulnerable, but it is more likely to be threatened by human impacts on its food base and habitats.
4.2 Human impacts on the African clawless otter

4.2.1 Direct conflict with humans

Otters are regarded as pests by the Tam Trout fish farm in the Burguret study area (Jonathan Bending, pers. comm) and are widely hunted for their fur, particularly in southern Africa. They are also known to eat young maize and vegetable plants grown near rivers and this is another source of conflict with humans (pers. Obs. 2004). They also get caught and drowned by funnel-mouthed fish traps, widely used in Africa. By and large, conflicts between otters and humans occur in cases where areas of human and otter activities overlap. Otters have been known to kill domestic poultry (Stuart & Stuart, 1994). People also kill and eat otters occasionally (pers. obs, 2004) but this is opportunistic, because the respondents indicated that they would not bother going out to hunt otters since it would be too difficult to find them. In South Africa, otters are regularly shot because they eat trout, which are an important source of income from sport fishermen in that country (Rogers, 2003). However, direct conflict with humans is a minor threat to otters in Kenya, but the most serious aspect of this threat may be the disturbance of otter dens by domestic dogs.

4.2.2. Indirect conflict with humans

These are the threats to otters as a result of human activities that impact negatively on the otters’ habitat and food base. They include deforestation, environmental pollution, and the introduction of invasive species that destabilize the aquatic ecosystems and compromise their productivity.

A prime example of the invasive species threat is the impact of crayfish (*Procambarus clarkii*) on aquatic fauna in Ewaso Ng’iro River. Prior to this study, *Procambarus clarkii* was thought to be incapable of establishing itself in running waters (Dobson, 2004) and its
effect on native crabs was unknown. This study has shown that the Louisiana crayfish can successfully invade a river and supplant the indigenous crab population by out-competing them for food. Competition between confined crabs and crayfish also showed that predation of crabs by crayfish may also be a factor. These findings indicate that crayfish have ramifying impacts on the structure and dynamics of aquatic ecosystems, thus concurring with the results reported by Lorman and Magnuson (1978) from Wisconsin, U.S.A and Harper et al., (1990) from Lake Naivasha, Kenya. The crayfish themselves would be a more adequate source of food for the otters, given the fact that their average weight based on specimens captured in the course of this study (17 grams) is significantly higher than that of the crabs (10.3 grams). The capture time for crayfish may actually be shorter because the Ewaso Ng’iro crayfish were observed to be strictly aquatic which reduces their escape options, unlike the crabs, which can hide in grass on the riverbanks and run fast over rocks. However, this factor has also been the mechanism through which the crayfish have proved harmful to the otters, because their vulnerability to predation has resulted in this food source being heavily exploited by other terrestrial and avian predators. Crayfish remains were found in the faeces of Baboons, genets, monitor lizards and herons. The otters have, therefore, had their niche exposed to competition by the crayfish invasion. The clawless otter population in the Ewaso Ng’iro drainage is particularly vulnerable to this kind of competition because their food base consists of small prey species that are not energetically profitable. This is at odds with the findings reported by Somers (2000) and van Der Zee (1981) on the Eastern Cape and Western Cape otter populations in South Africa.

The Burguret River was initially considered to be relatively ‘pristine’ compared to the lower Ewaso Ng’iro because of the lower water temperatures (average daily maximum<12
degrees centigrade) that do not allow crayfish to survive there. However, examination of stomach contents of 51 trout revealed that the fish is a potentially threatening invasive species because of the trout’ dependence on crabs as prey. This concurred with Dobson (2004) and Williams et. al. (1964), who found that both the brown trout (Salmo trutta) and the rainbow trout (Oncorhynchus mykiss) caused reduction in crab numbers through predation. The impact of trout on the crab population in the study area could be magnified by the fact that they are mainly preying on juvenile crabs, thus affecting recruitment. This study found that deforestation is a major threat to otters, particularly in the ‘pristine’ highland aquatic ecosystems. The low crayfish content in faecal pellets collected at high river levels showed that crustaceans were more difficult to capture in turbid water. These tend to be fast-flowing rivers with steep banks like the Burguret, and the deforestation leads to increased erosion and siltation. These rivers generally have clear water, and siltation will cause increased turbidity. The turbidity of the water will not directly affect the prey (crab) population, but it will increase the search time and consequently the amount of energy spent per unit prey captured. In otter populations living on small prey species like (P. neumanni), any change in the abundance or accessibility of prey could push the required foraging time beyond sustainable levels. This would lead to local extinction because otters would not have time to mark territory, prepare dens, find mates and rear young. This concurs with Giller and Malmqvist (1998) who reported that most the serious threat to unique animal and plant species in running water ecosystems is human-related habitat degradation, leading to increased silt load in rivers. Another mechanism through which deforestation can threaten otter populations is through the increase in water temperatures.
Moss (1998) found that deforestation may raise stream temperatures due to removal of shading. In the Ewaso Ng’iro ecosystem scenario, this could open up the upstream reaches to the crayfish invasion.

4.2.3 Positive human impacts

Generally speaking, human impacts on wild habitats tend to be negative, but in a few instances can be positive. In shallow rivers like the Ewaso Ng’iro, small dams that were built as water reservoirs for livestock ranches preserved deep-water habitats, particularly during the dry seasons, when water level dropped below 40cm. This study found that in the post crayfish invasion scenario, these dams provide refuges from which crayfish populations recover from the heavy predation that occurs during the dry season. Evidence of this feature can be seen in the lower Ewaso Ng’iro otter territories. Every water reservoir in the northern study area was at the centre of an otter territory. It can also be recognized from the relatively high crayfish content in otter faecal pellets maintained during the dry season when pellets in the other areas had higher proportions of fish. Water depth was also found to influence the distribution of crayfish in streams in Missouri, U.S.A., with the larger crayfish using the deeper areas (Rabeni et al., 1995). Artificial water reservoirs are, therefore, very important to otter populations in riverine ecosystems where their food niche has been compromised.

4.2.4. Weight distribution of Ewaso Ng’iro crayfish

An examination of the weight class distribution of trap sampled crayfish indicates that the highest number weighed between 20-40 grams. The 4th largest weight class was the 5-12.5 gram weight class. This class does not feature as prominently in the weight distribution of
crayfish eaten by otters. This is probably because in turbid rivers like the Ewaso Ng’iro, otters forage mostly by touch, using their forefeet and long vibrissae. The probability of detection is therefore proportional to the size of the crayfish. The larger crayfish have a higher probability of detection, so their low representation in the otter diet might be an indication that this class is the most heavily exploited by different non-otter predators.

Mature Louisiana crayfish regularly attain weights of over 72 grams (Hobbs et al., 1989) and when the otters are mostly exploiting the 13.5-20.5 gram class, it indicates that they are beginning to rely on juveniles due to increased and competition and the consequent scarcity of crayfish from the higher weight classes. Exploitation of this pre-reproductive class affects recruitment and is not sustainable in the long term. This is illustrated by the decline in Ewaso Ng’iro crayfish abundance which is likely to lead to the local extinction of otters. The lower Ewaso Ng’iro study area remains in transition and further research will be needed to determine whether crabs and eventually otters will fully re-colonize the area.

4.3 Diet of otters in the study area

Crustacean prey was the most important food item for otters in the study area. Various cyprinid and cichlid fish species are widely available throughout the Ewaso Ng’iro ecosystem and are more profitable food items for the otters. The otters’ dependency on crustaceans is a pointer to the difficulty otters have in catching fish due to their lack of claws. Therefore, it follows that a high proportion of fish in otter scats is an indication of food stress in the otter population. Traces of ungulate dung have been reported to occur in otter scats (Rowe-Rowe, 1977a) but this phenomenon was neither investigated nor discussed in that publication. In the current study, ungulate dung was only found in scats containing 70% or more of fish. The same scats were also found to contain remains of
coleoptera. Ungulate dung is most likely ingested by otters as they eat dung beetles from dung piles on the riverbanks.

4.3.1 Effect of water levels on otter diet

Water levels in the lower Ewaso Ng’iro study area had an influence on otter dietary content. Analysis of crayfish content in otter scats and river levels by lowess curve at tension level 66 showed parallel trend (Fig.10). Since otters eat crustacean prey by choice (Rowe-Rowe 1977b), this trend can be reliably used as an indicator of crayfish availability. At the end of the study, a gradual discrepancy was beginning to arise between the river levels and the proportion of crayfish in the otter diet. This was caused by the overall net decline in the crayfish population. At this stage, the trap sampling yield in the Ewaso Ng’iro had declined to a level of zero per trap night. The otters were still able to find crayfish because they were actively searching, unlike the traps, which are passive. A threshold depth of 38 cm was identified above which the three major indicators of otter territorial behaviour and nutrition were highest. The indicators were; the mean crayfish content in the faecal pellets, the number of the faecal pellets collected per unit time, and the percentage of aggregated faecal pellets. These indicators declined as water levels rose beyond 45cm. The observed competitors for crayfish were then closely examined in an effort to identify the mechanism driving the steep decline in crustacean prey availability below the 38 cm threshold. Four species were observed: the Olive baboon, the Nile monitor lizard, the black-headed heron and the grey heron. This contrasts with reports from the Western Cape, South Africa (Somers, 2000) which did not identify any terrestrial competitors for the otters’ niche in the surf zone, despite the presence of yellow baboons Papio cynocephalus in the area. The monitor lizard is a strong swimmer, which was able to easily cross and forage in the Ewaso
Ng'iro river even at the maximum depth of 3.5 meters. Their access to crayfish would therefore not be changed significantly by a depth increase of 5 cm, which eliminated them as a key competitor to the otters. The olive baboon grows to a height of approximately 55 cm at the shoulder (Kingdon, 1997), so theoretically they would be able to reach crayfish at a depth of 50 cm. In reality, however, their limit may be significantly lower than that because of the difficulty in seeing crayfish through the turbid water. The crayfish eating behaviour was only observed in one troop of baboons at the confluence of the Ewaso Narok and Ewaso Ng’iro rivers. Even though primates are quick to learn new behaviours, crayfish consumption by baboons is currently at a level which is unlikely to impact on the overall Ewaso Ng’iro crayfish population. There were 3 heron species present in the lower Ewaso Ng’iro namely, the goliath heron, grey heron, and black-headed heron (Zimmermann et. al., 1999). The goliath heron (Ardea goliath) was the largest of the 3 species with an average leg length of 62.5 cm and feathering at 53 cm. They could, therefore, be able to prey on crayfish at a depth of at least 50 cm. It was consequently eliminated as a possible factor causing the 38 cm threshold beyond which the otter faecal pellet collections rose drastically. The grey heron (Ardea cinerea) was another predator of crayfish present in the lower Ewaso Ng’iro. The mean leg length of specimens at the National Museums of Kenya was 37 cm. It would, therefore, be a potential influence behind the 38cm threshold. However, this species is listed as uncommon, and favouring wetlands, brackish alkaline lakes, and coastal flats (Zimmerman et al., 1999). None of these habitats was present in the study area and most of the Laikipia Plateau is arid, so this eliminated the species because the study area did not consist of its preferred habitat. The Black headed heron (Ardea melanoccephala) specimens had a mean leg length of 39.5cm and this would enable them to forage up to the 38cm threshold. This is the commonest and most widely distributed East African heron and it is
not restricted to littoral or aquatic habitats (Zimmerman et al., 1999). It can live in arid habitats, hunting insects and rodents and it was the most commonly observed heron in the study area during this study. The above factors identified the black headed heron as the species determining the 38cm threshold beyond which the proportion of crustacean remains in faecal pellets increased. Water levels in the Ewaso Ng’iro rise very suddenly with the onset of rains in the Aberdare Mountains and Mt Kenya. The brevity of this transition period is the reason for the low number of faecal pellets collected between the 45-55 cm river levels.

In the Burguret study area, there was no significant effect of water levels on the otters’ nutrition, despite the fact that the river water level dropped as low as 10cm during the dry season and never rose beyond the 35cm mark during the study period. The Burguret otter population did face competition for crabs as well. Crab remains were found in baboon scats and pellets regurgitated by the Mackinder’s eagle owl (Bubo capensis mackinderi). The impact of these two species on the crab population was mitigated by the crabs’ ability to take refuge from them under water. The greatest potential threat to the crab population in the Burguret river is the exotic brown trout. Adult crabs can escape from this threat by moving out of the water onto rocks or the riverbank, but trout prey mostly on juveniles, which are restricted to the water. This factor could curtail recruitment, thus impacting on the crab population and consequently the otter population.

4.4 Otter habitat quality in the study area

The assessment of this variable was based on the availability of crustacean prey because the small size of the prey species compelled otters to spend most of their time foraging. Otters in the study area need to eat 85.357 crabs daily or 3.55 crabs per hour to meet their
nutritional needs, presuming 24 waking hours (which is an ideal unachievable in nature). In the lower Ewaso Ng’iro, proportion of crayfish in faecal pellets was found to decline at lower river levels. Relatively high proportions of crustacean (crayfish) remains in faecal pellets at lower river levels were, therefore, taken to be indicators of higher otter habitat quality. The high quality otter habitats in the lower Ewaso Ng’iro coincided with four deep water pools. This indicated that the high quality otter habitats were formed by deep water refuges where crayfish could be safe from the non-aquatic predators, the largest of these being the Mpala Ranch Dam. Most faecal pellets were collected around these points during the dry season, indicating that otter activity was concentrated there, regardless of the regular boundaries of the family groups’ territories. The intersection of the lines indicates the point where otter habitat quality has deteriorated to a level where it is no longer influenced by water level. The geographical location of this point was the confluence of the Ewaso Ng’iro and Ewaso Narok river (the Northern limit of the study area). Maps showing the distribution of otter faecal pellets during the study period indicated that by the December 2004, the remaining otters seemed to be using the Mpala Ranch Dam, suggesting that this was the last consistent source of crayfish. This was consistent with the findings of Rabeni et al. (1995).

A similar comparison was done on the Burguret study area using the 20cm river level as a threshold. There was no significant difference in the proportion of crustacean (crab) remains in faecal pellets collected either side of the threshold as was indicated by the lowess curve at tension value 66. The lines were highly parallel and Simple regression at 95% confidence interval to get exact trends yielded slightly divergent lines (Crab% = 1956.361 - 1.861E-4 * UTM; R^2 = 0.0005968 and Crab% = 16521.345 - 0.002 * UTM; R^2 = 0.004). This indicates that the Burguret River level did not influence the proportion of crab on otter faecal pellets. This is because crabs voluntarily left the water and this ‘amphibious’ nature
meant that even though they were being eaten by non-aquatic predators, their susceptibility to predation did not change with river levels. A high level of terrestrial activity in most East African freshwater crabs was also reported by Morris & van Aardt (1998). Prey availability was used to assess otter habitat quality in this study because this was the factor that differed most through the study area. Abiotic factors were not found to vary significantly through the study area with the exception of temperature and water depth. Analysis of these variables by ordination and classification (Begon et al., 1996) was found to be inappropriate because this method does not give any measurement of trends. It is also inaccurate to assign chemical properties like pH to a specific point in flowing waters.

4.5 Otter and crustacean population trends in the study area

There was a net increase of 6.388% in otter population density in the Burguret study area during this study as estimated from faecal pellet collections. This corresponded with a 17.14% decrease in crab abundance as estimated from trap sampling yield during the same period. In the lower Ewaso Ng’iro study area, there was an 80.7% decrease in otter population density during the study period, accompanied by a 98.7% decrease in the abundance of crayfish as estimated from the trap sampling yield. The two variables were positively related, but the relation was not statistically significant. However, this was an indication that the decline in otter population density was driven by the declining abundance of crayfish. The discrepancy between the two rates was due to the fact that such a trend would be reflected more immediately in the yield from a passive trap than the number captured by an active predator. These results are consistent with the findings of van Der Zee (1982) who reported that the density of (*Aonyx capensis*) in the Eastern Cape, South Africa, was influenced by the availability of food resources. However, the Ewaso Ng’iro trend
pointed to a local extinction within 34 months from the beginning of this study, i.e. by October 2005. At present, crayfish are still present in the Lower Ewaso Ng'iro as deduced from otter faecal pellets, but trap sampling yields in the study area had declined to zero per trap night. In August 2004, crayfish remains were identified from an otter faecal pellet collected in the Burguret study area. Experiments with captive crayfish placed in the water at this location still died within 8 hours due to the low temperature, eliminating the possibility of invasion. This shows that the source of the pellet was an otter immigrating from the downstream area below the 14 degrees centigrade threshold. This is a distance of approximately 14 km covered by the otter in 24 hours, which is well within reach for otters, which can travel up to 13 km per night (Maxwell, 1960). It is also an indication that the decline in the lower Ewaso Ng'iro otter population is occasioned by emigration of otters upstream to more productive habitats. The apparent increase in the Burguret otter population density could also be an indicator of the same. This event implies that the spread of the Louisiana crayfish constitutes a serious threat to the survival of otter populations in riverine habitats. In Kenya, the only otter populations relatively ‘safe’ from this threat are those of in Lake Naivasha and Lake Victoria (Kruuk & Goudswaard, 1990), both of which are heavily impacted by other human activities. The densities estimated in this study are considered to be maximum densities because they are based on the assumption that territories are being marked and defended by family groups (Kingdon, 1977) and not individuals.

4.6 Nutrition of otters in the study area
The nutritional status of otters living in the Ewaso Ng’iro drainage (including the Burguret) is highly vulnerable. They are living on very small prey species, which must be easily available to them in large quantities with minimum energy expenditure per unit prey caught. Based on prey requirement calculations by Schaller (1972), an average (18 kg) otter would need to consume 320.9 kg of prey per annum or 879 grams daily. In the Burguret study area, the estimated amount of crab eaten per otter was 20.1086 grams. However, these figures are also likely to be an underestimation due to various factors, including the faecal pellets getting washed away by seasonal flash floods and rains, which are very frequent and heavy in the Mt Kenya forest. Another source of error is the difficulty in detecting randomly placed faecal pellets during the dry season when territorial marking behaviour breaks down, particularly in the lower Ewaso Ng’iro study area. In the lower Ewaso Ng’iro study area, estimations from remains in faecal pellets indicated that otters were getting only 0.91777 grams of crayfish daily. Since crayfish formed 60% of their diet, analysis of faecal pellets indicated that each otter was consuming 1.5296 grams of prey daily. This was also an underestimate due to the reasons stated above. However, given that there were similar environmental factors influencing the retrieval of faecal pellets in both areas, the factor of underestimation (sources and degrees of error) were taken to be the same. The crucial indication here is that otters in the Burguret River are able to access 13.146 times as much food as the otters in the lower Ewaso Ng’iro. The actual difference in the productivity of the 2 ecosystems is even higher when the disparity in otter population densities is taken into account. This ‘crash’ in productivity has occurred within 15 years of the first recorded evidence of crayfish in otter faecal pellets (Kruuk & Goudswaard, 1990). Assuming that the otters in the Burguret study area are getting adequate nutrition, the otters in the lower Ewaso Ng’iro are getting far less than what they would require to mark territories, prepare dens and
raise young. It is, therefore, unlikely that this population has had any recruitment for the last 7 years, since the productivity of their environment fell below 50% of what it was in the original ‘pristine’ condition. This is indicated by the decline in faecal pellet collection.

4.7 Impact of the Louisiana crayfish on the Ewaso Ng’iro ecosystem

Experimental competition between captive crabs and crayfish showed that crayfish are physically superior competitors to the freshwater crabs. When equal numbers of crabs and crayfish were placed in a cage, all crabs were killed within 60 hours and thereafter eaten by the crayfish. However, when there were rocks placed in the tank, the crabs were able to escape from the crayfish by climbing out of the water onto the rocks, which significantly reduced the rate at which they were captured and killed by the crayfish. This gave an insight into the possible mechanism by which the crayfish have supplanted the freshwater crab in the Ewaso Ng’iro River. In the wild, the crabs would have been able to climb out of the water onto rocks, but this would have exposed them to predation by terrestrial and avian predators other than the otters. The difference in the two crustacean species’ susceptibilities to predation at low water levels is crucial to understanding the effect of the crayfish invasion on otters in the Ewaso Ng’iro ecosystem.

Analysis of crayfish proportion in otter faecal pellets and river water levels by lowess curve showed parallel trends in the two variables throughout the year 2003. Disparity between the two began to show at collection number 352, which was on the 1st of March, 2004. The subsequent rise in river levels was not accompanied by a corresponding rise in crayfish content. This phenomenon likely identifies the point at which the Allee effect (Begon et al., 1996) began to take place in the crayfish population. The Lower Ewaso Ng’iro ecosystem does not appear to have achieved any sort of ‘equilibrium’ since being disrupted by the
Louisiana crayfish invasion. This is illustrated by the local extinction of the freshwater crab, and the downward trend in the population of the African clawless otter. An examination of the number of different aquatic species captured in sampling traps in February, 2003 and November 2004 indicates a sharp decline in Ewaso Ng’iro aquatic biodiversity. Initially, there were 3 classes and 12 species identified from sampling yields in the Ewaso Ng’iro area. In November 2004, there were only 3 species representing one class (osteichthyes) and one family (cyprinidae). This is a loss of 75%, but it must be noted that the sampling trap was made from 1.875 cm gauge wire mesh and the data is representative only of organisms larger than this. The actual number of species lost may therefore be higher. The vulnerability of the Ewaso Ng’iro otters’ food base contrasts greatly with that of the Tsitsikama otters where a total of 33 prey species from 4 classes were identified from scat analysis (van Der Zee, 1981). Linear regression of the rate of decline in crayfish content in faecal pellets against the faecal pellet collections indicates that crayfish content would reach zero by collection number 1896. An extrapolation of current collection rates theoretically points to that number being achieved within seven years from the beginning of the study (January, 2010). This could occur sooner as the numbers of terrestrial and avian predators of crayfish increase. This is a likely scenario as more individuals within each predator species discover this new resource. Time frames can only be confirmed by continuous monitoring, but it is a certainty that all 3 species being studied in this project will undergo local extinction in the Ewaso Ng’iro in the course of this ‘cycle’. The freshwater crab has been put under predation pressure by the invasive Louisiana crayfish, which in turn has been preyed upon by otters and other terrestrial and avian predators. In the final analysis, the otter population is unlikely to survive without a secure food niche in the lower Ewaso
Ng’iro ecosystem. The crustacean food niche has apparently been compromised, so the otters’ future would seem to be dependent on their ability to switch to a different prey base.
CHAPTER 5. CONCLUSIONS

This study has established that ecological disturbances that affect the prey base for *Aonyx capensis* are the biggest threat to its population throughout its range. A readily measurable indicator of the relative ‘safety’ of other otter populations from this threat is the width of variety in their diet. An examination of the diet of otters in the Tsitsikama Coastal National Park in South Africa revealed this. There were 33 different prey species identified from otter scats within a year excluding insecta. In the lower Ewaso Ng’iro area, there were 7 prey species identified excluding those of class insecta. In the Burguret area, there were only 3. In Tsitsikama, it would take a very broad-spectrum event like an oil spill to disrupt the otters’ food base to a threatening level. However, in the Burguret river and similar habitats where crabs comprise 98% of the otters’ diet, even a very narrow or highly specific threat like a virus affecting crustaceans could extirpate the local otter population very rapidly. This leads to the conclusion that otters in Kenya are extremely vulnerable, particularly in the habitats that appear to be their ‘strongholds’. Given that these are the ‘pristine’ or relatively intact habitats, the future of otter populations in Kenya is highly uncertain due to ecological threats to their habitats.

The study has also revealed that immediate preventive measures are the only available options to curb this type of threat to the African clawless otter because the environmental effects of alien species are virtually impossible to undo. This species may therefore be lost forever from the lower Ewaso Ng’iro unless the current cycle continues and crayfish are eliminated, giving the crabs a chance to recolonize the area.

Based on proportions of crayfish found in otter faecal pellets by Kruuk and Goudswaard (1990), the initial (*Procambarus clarkii*) invasion in the Ewaso Ng’iro ecosystem occurred less than 20 years ago, probably between 1986 and 1988.
This study also found the Louisiana crayfish has directly caused the local extinction of the freshwater crab (*P. neumannii*) in the lower Ewaso Ng’iro through predation and competition for resources. Through interaction with various biotic and abiotic factors it has caused the decline of the African clawless otter in this habitat.

**Stage 1:** Dry Season. Low water level due to drought, water extraction

**Stage 2:** Crayfish exposed to herons, genets, baboons, etc (otters’ niche invaded)

**Stage 3:** Otters experience food stress and territorial behaviour breaks down.

**Stage 4:** Rainy season. High water level. Otters’ niche re-established. Territorial marking resumes.

**Figure 29. Post-invasion dynamics of otters and crayfish in the Ewaso Ng’iro ecosystem**

Initially, these events appear to form a perpetual cycle (Fig. 29) that can continue indefinitely, with all things remaining equal, but this is not the case in the Ewaso Ng’iro ecosystem. Due to cognitive learning, the number of individual terrestrial and avian predators exploiting crayfish increases in every subsequent dry season, thus applying more pressure to the crayfish population. Considering the indirect nature of its impact on the
otter, it is remarkable that the crayfish could precipitate the otter’s local extinction in less than 20 years. However, the process is likely to have been accelerated by the long drought of 2000-2001, which was caused by the ‘La Nina’ event. This caused an extended ‘dry season’ lasting for approximately one year. The prolonged exposure of crayfish in shallow water and decline of terrestrial prey species would have caused more terrestrial and avian predators to learn about and exploit this new food source. This study, therefore, concludes that many species and abiotic factors have been involved in the decline of the African clawless otter in the Ewaso Ng’iro, but \textit{(Procambarus clarkii)} is the root cause.

Few respondents in the study area were familiar with the African clawless otter or aware of its existence therein. During the study period, however, there was one recorded incident of an otter being opportunistically killed and eaten by local people and one report of otters eating vegetables from a plot on the riverbank. Both of these occurred in the Burguret study area. Consequently, there was no significant direct conflict between otters and people and the impacts examined were all indirect.

This study has found the dams built as water reservoirs on the Ewaso Ng’iro River by ranchers to be a positive human impact on the otter population. The dams are used as water reservoirs by livestock ranches in the Laikipia Plateau and in the lower Ewaso Ng’iro, they formed deep water refuges for crayfish during the dry season (Fig. 15). This was indicated by the relatively stable proportions of crayfish in faecal pellets collected from these points. These points also retained a relatively high level of faecal pellet aggregation during the dry seasons when otter territorial behaviour broke down. All the three otter territories identified in the lower Ewaso Ng’iro study area included dams.

The major human impact on otters in the study area has been the invasion of the Louisiana crayfish, which has been negative. Given that interspecific competition crayfish
and other crustaceans is the mechanism by which the crayfish has impacted the Ewaso Ng'iro otter population, it is bound to have affected other species as well. This would be especially true of the species that have been competing with the otters for this food resource. Were it not for the crayfish invasion of the lower Ewaso Ng’iro study area, the positive impact of deep water refuges would not have been felt by the otter population, so human activities have had an overall negative impact on otters in the study area. In conclusion, the otter population in the lower Ewaso Ng’iro area and the ecosystem as a whole has been severely compromised by the Louisiana crayfish invasion and only more research can reveal whether either of them will recover.

This study found the Burguret study area to be relatively pristine at present, but still needs protection in the long term. Crayfish were excluded from the Burguret study by the low maximum water temperatures, but there were (exotic) brown trout introduced into upstream areas for sport fishing. Some trout also occasionally escape from the TamTrout fish farm at the northern end of the Burguret study area. Human impacts in this area, therefore, cover the scopes of both biotic and abiotic factors. Relative to the Ewaso Ng’iro study area, otters were successful in the Burguret River and population densities were significantly higher. There was one artificial water reservoir in this area, but there was no detectable difference in the composition or aggregation of scats collected there. Potential threats to otters noted here include deforestation on the banks of the Burguret River, which increased drastically during the study period. This will increase soil erosion during the frequent heavy rains and result in siltation of the water. Turbidity of the water will increase the search time for foraging otters and consequently compromise the availability of food, without necessarily reducing the abundance of the prey base. Otters do forage by sight, but those observed in the Burguret area do not appear to have very good eyesight. When
emerging from the water, Burguret otters appeared unable to see a person sitting on the riverbank even at a distance of 3 meters away. This indicates that a change in turbidity will rapidly and drastically affect the otters’ ability to fulfill their nutritional requirements. African clawless otters are known to dig dens among the roots of trees on riverbanks. Destruction of trees in the otters’ habitat, would therefore deprive them of denning sites, which are essential for shelter. Even with ample food supplies, otters like most other carnivores give birth to helpless vulnerable young that cannot be raised without secure shelter.

Deforestation and consequent exposure of rivers to solar radiation can also raise water temperatures significantly. This would be especially true at the Burguret river, which is approximately 17 km south of the Equator. A rise of 3 degrees Centigrade in the mean maximum water temperature would expose the Burguret River to invasion by crayfish. The Louisiana crayfish is known to have successfully invaded mainland Europe, and adapted to temperatures lower than those in the Burguret study area, so the threat to this ecosystem remains, even without a rise in water temperature.

The other potential threat in this area is interspecific competition for the crab food base from the brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*). This is because crabs form 98% of the otters’ diet in the Burguret study area, as opposed to 60% formed by crayfish in the lower Ewaso Ng’iro area.

This study, therefore, concludes that the Burguret River and similar highland rivers are relatively intact but very fragile otter habitats that can easily be compromised. The importance of these habitats is underscored by the fact that most lowland river habitats in Kenya are already heavily exploited and damaged by human activities.
CHAPTER 6: RECOMMENDATIONS

6.1 Remedial actions

a) A concerted effort to remove crayfish from pools in the Ewaso Ng‘iro river during the dry season should be undertaken. The reproduction and dispersal of alien species beyond the point of origin makes the effects of biological invasions largely irreversible (Allan, 1995). As far as the Ewaso Ng‘iro River is concerned, the only possibility of recovery is if the current cycle continues, resulting in the local extinction of crayfish. In resource-depressed systems, crayfish congregate in pooled areas of streams and rivers. This behaviour is also reflected by the assessment of otter habitat quality in the lower Ewaso Ng‘iro study area. Long-term trapping concentrated in these pools could depress crayfish populations over time. This would theoretically allow for recolonization of the habitat by crabs and consequently otters.

b) Fish exporters should diversify their range of products from Kenya to include crayfish. Kenya was exporting 500 tons of crayfish to Europe annually by 1988 (Holdich & Lowery, 1988), but this declined to 6 tons by 2002 (Fisheries Dept. Annual Report, 2002). The provision of a market could lead to increased exploitation, thus controlling populations. The livestock feeds industry should also exploit crayfish for use in high-protein supplements. This could be a viable alternative to fishmeal which is becoming more difficult to obtain, due to the countrywide decline in fish stocks. However, aquaculture of crayfish should not be licensed, since this could lead to further introductions into uninvaded aquatic systems. Exporters could instead exploit wild populations, thereby maintaining their
business while mitigating the long-term ecological impacts of crayfish in aquatic systems.

c) The Tam Trout fish farm (and all other hatcheries rearing exotic species) should install effective barriers to prevent the escape of trout from the tanks. This occurs due to flooding during the rainy season.

d) There must be a concerted effort to remove the brown trout that have entered the Burguret River ecosystem. This can be done by encouraging the use of fish traps by locals to catch as many of them as possible. A combination of this, and predation by otters would keep pressure on the trout and prevent their numbers from reaching levels that are competitive for the otter prey base.

6.2 Preventive policy action on species introductions.

a) The National Environmental Management Authority (NEMA) should immediately expand the scope of its monitoring activities to cover biological invasions as well as physical and chemical threats to the environment, especially aquatic systems.

b) Fisheries authorities should ban all stocking of aquatic habitats with non-indigenous species for sport or commercial fishing.

c) Fish farming should be restricted to indigenous species in future to avoid biological invasions caused by escapes and flooding.

d) Strict quarantine standards should be prescribed by the Fisheries Department to all fish farms rearing exotic species and the department should also monitor surrounding waters for escapees.
e) The Ministry of Environment should put in place strict legal regulations governing and restricting all species introductions

6.3 Further Research

6.3.1 Overall status of Aonyx capensis population

Further studies are urgently required to establish the overall status and distribution of (A.capensis) This species is not listed as endangered or threatened by the IUCN. This is due to data deficiency. Available data only indicates presence or absence, but there are no estimates of numbers left in the wild, or limits of their range. This study has shown that they are a very vulnerable species, particularly in riverine habitats because of their narrow prey base that magnifies the effects of environmental disturbances on their nutrition. There is an urgent need to estimate population densities by collection of scats over time. This is a relatively simple task due to the linear nature of riverine habitats.

Further research is also needed to come up with a comprehensive list of all the biotic and abiotic factors that are vital for survival of otter populations. The impact of changes in these factors on otter populations should also be measured. This would enable scientists to ‘calibrate’ the environmental factors so that changes in the otter population can be estimated or extrapolated from data gathered by environmental monitoring. Results of this study indicate that highland rivers with cold water are important refuges for otter populations now and in the future. It is important to thoroughly survey the highlands of Eastern Ethiopia, which have not been covered by the distribution map given by Kingdon (1997). Thorough population surveys are also an urgent priority because judging also from the results of this study, A. capensis is fast disappearing from lowland riverine habitats. This is because of natural and man-made threats. Widespread deforestation in Africa has also resulted in the
siltation of lowland rivers and their estuaries. This would increase the search time for foraging otters beyond energetically sustainable levels. The River Tana is included in the Kingdon’s (1997) distribution map, but based on the current condition of that river and the crocodile density there, it is very unlikely that *A. capensis* can still be found there. This study therefore recommends not only surveys to find previously unknown otter habitats, but also surveys to ascertain their continued existence in habitats where they have been recorded previously. Telemetry studies on *A. capensis* thus far have only been done in coastal habitats. This needs to be done in riverine habitats to confirm territory sizes and further calibrate the ‘scats and glue’ method (Ogada, 2004). This would also indicate how far otters can move in search of new territories or more productive habitats.

Longer term research is also required on otters in the Ewaso Ng’iro ecosystem. This study predicted local extinction of otters by late 2005, but the reality is that otters are still persisting, particularly in the northern areas where the crayfish density was low during the course of this study. The reality is that the otters have switched from the crustacean diet and the average percentage of fish in faecal pellets has now risen to 85%. Extrapolation has its limitations and only long-term research can result in absolute certainty.

### 6.3.2 Otter Research Methods

Further research should be done to develop accurate and cost effective research methods for studying otters. *Aonyx capensis* is a difficult animal to study in the field. This fact is reflected in the very small number of published studies on its ecology. All studies on this species thus far have been done only in South Africa and Zimbabwe, which form only approximately 14% of its known range. Standard methods commonly used for field studies of terrestrial carnivores are generally not applicable to otters, and herein lies the difficulty. For example, they cannot be fitted with radio collars because the neck is actually thicker
than the head. Transmitters, therefore, have to be implanted subcutaneously in a risky and invasive procedure. They also cannot be marked using plastic ear or toe tags because they can pull these off using their forefeet or ‘fingers’. They are also highly intelligent animals, which are very difficult to trap, and the highest recorded success rate is 8% achieved by Arden-Clarke (1986). This study recorded a success rate of only 1.66%. This may have been due to the reluctance of otters to enter cage traps, but foothold traps could not be used because captured animals would be attacked and eaten by hyenas or leopards. Studies of otters, therefore, demand a high level of improvisation. One important method to come out of this study is the ‘scats and glue’ method for mapping territories (Ogada, 2004). However, more research needs to be done on how to apply this method to lakes, coastal, and estuarine habitats. Van der Zee (1982) used scats at holts to estimate otter population density, yielding a figure of 1 otter per 2.7-3.9 km. This is likely to be an underestimation because in Tsitsikama, food is plentiful and territorial marking at holts is likely to be solely done by males for mating purposes. In the Ewaso Ng’iro River, territorial behaviour is more likely to be resource-driven due to periodical food stress. Such differences underscore the need for studies to experimentally apply field methods in different habitats.

Ecological research on river ecosystems must include terrestrial and avian species that exploit river resources. Aquatic ecological studies currently tend to exclude terrestrial fauna and vice versa, thus missing very important links in food chains. Since the African clawless otter is basically a terrestrial animal that forages in water, this study has managed to capture a picture of the complex relationships between aquatic and terrestrial fauna. Some of these would escape an exclusively aquatic or terrestrial study, so there is need to develop an ecological field of study that properly recognizes and investigates this continuum.
6.3.3. The Ewaso Ng’iro ecosystem.

The Ewaso Ng’iro ecosystem is undergoing a transition and it is vital that the data collection done for purposes of this study be continued in the long term for at least the next five years in order to address the following research issues;

a) Whether or not the Louisiana crayfish will finally become locally extinct in the Ewaso Ng’iro due to predation pressure.

b) How the dynamics of the Louisiana crayfish will affect the populations of the terrestrial and avian predators that have been exploiting it as a food source.

c) Whether or not the freshwater crab *Potamonautes neumannii* population will recover due to predation pressure on the Louisiana crayfish population?

d) Whether or not the changes in the crustacean community will lead to a re-colonization of the study area by otters.

e) Thorough environmental monitoring programs must be put in place to monitor the water condition of the Ewaso Ng’iro and as many other freshwater ecosystems as possible. Current programs consist only of river level gauges. The database must be expanded to include temperature and chemical properties e.g. pH and conductivity. This would alert scientists and managers to changes in conditions that could damage ecosystems, either by killing indigenous species or expanding geographical boundaries of species invasions.

6.3.4 The marsh mongoose

Further research is required to establish the distribution and status of the marsh mongoose (*Atilax paludinosus*). This species is known to be ecologically the closest competitor to the African clawless otter and the 35% niche separation is due only to the otters’ diving capability. Studies in Natal, South Africa showed that the two species have a
65% food overlap (Rowe-Rowe, 1977a). Freshwater crabs and frogs are major items in the diet of *Atilax* (Kingdon, 1997) and are usually taken from the riverbanks and marshes. The Louisiana crayfish could theoretically impact heavily on this species by predation on crabs and tadpoles. During the course of this study, marsh mongoose was last observed in the lower Ewaso Ng’iro study area on March 11th 2003. Faecal pellets from *Atilax* were last collected in the study area on 13th October, 2003. Research needs to be done to ascertain whether this is an indication of a local extinction. If this is the case, it could mean that they are more sensitive indicators than *Aonyx* of aquatic ecosystem productivity.

6.3.5 The Nile monitor lizard.

Further research is required on the dietary trends of this species in the lower Ewaso Ng’iro. It is a generalist predator whose diet may indicate overall aquatic community dynamics, rather than the availability of only crustaceans, as is the case with the otter’s diet. Dissection of specimens opportunistically caught in the study area revealed that crayfish formed the largest single portion of the monitor lizards’ diet in the lower Ewaso Ng’iro study area. They have a widely varied diet, but are fond of freshwater crabs, which they crush with their peg-like teeth (Spawls *et al.*, 2002). They will also take any available vertebrate or invertebrate prey. The availability of an abundant crustacean food source (Louisiana crayfish) may have caused a rise in the population of monitor lizards in the study area. Further research is needed to determine how the crayfish invasion impacted the monitor lizard population the rest of its prey base.

6.4 The Louisiana crayfish invasion

There is urgent need for a rapid survey of aquatic ecosystems countrywide to ascertain the geographical extent of the crayfish invasion in Kenya. It is important that this is assessed as a matter of urgency because crayfish are generally the largest and longest-lived crustaceans
in freshwater ecosystems and they process temporally and spatially large quantities of organic matter (Thorp & Covich, 2001). They function mainly as opportunistic generalists, and once established in an ecosystem, they feed at virtually all trophic levels, consuming all available organic matter including small aquatic fauna, aquatic plants, and detritus. In the underwater real, crayfish have been shown to reduce species richness and biomass of aquatic vegetation by selective grazing (Lorman & Magnuson, 1978). Crayfish also reduce the diversity of aquatic fauna by consuming significant quantities of fish eggs, as well as the eggs of other crustaceans (Horns & Magnuson, 1981). They have also been shown to reduce snail population in lakes and streams (Lorman & Magnuson, 1978). This feature led to the ill-advised use of crayfish as a biological control for schistosome transmitting snails in Kenya (Mkoji et. al., 1990).

This study on the Ewaso Ng’iro ecosystem has demonstrated that crayfish will also have an impact on the mammals, birds, and reptile that prey on them. It is, therefore, impossible to overstate the impact of crayfish on aquatic ecosystems. Further studies also need to be done to determine the effect of crayfish on bird and monitor lizard populations. This is particularly important in rivers like the Ewaso Ng’iro, which has undergone a cycle that includes disappearance of the crayfish after the initial damage inflicted on the ecosystem.

Research also needs to be done to determine whether crayfish are ‘vehicles’ that could lead to bio-accumulation of pollutants in the tissues of tertiary consumers eating them e.g. otters and herons. Benthic organisms are known to accumulate higher amounts of heavy metals than other aquatic fauna. Female (P. clarkii) are generally larger and more tolerant of mercury than males. Larger crayfish (which form the larger part of otter diet due to higher likelihood of being caught) were able to withstand higher concentrations of mercury. The
females could withstand up to 30 days exposure to $10^{-6}$ M HgCL for 30 days while males had 50% mortality after 3 days (Mason, 1981).

Thorough investigation of (*P. clarkii*), its geographical range in Kenya, and its effect on aquatic, littoral and terrestrial ecosystems will provide the right tools to limit its spread and mitigate the effects thereof. In this way we can maintain healthy aquatic ecosystems which are vital for the survival of otters in Kenya.
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