

# Predation Capability of Black Kite (*Milvus migrans parasitus*) on Locust as a Biological Control Option in Madagascar

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## Abstract

In Madagascar, the South and Southwest regions have for decades had locust outbreaks that have devastated crop fields. The locust species dominant in this area are the red locust (*Nomadacris septemfasciata*) and the Migratory Locust (*Locusta migratoria capito*). This paper aimed at determining the predation values from the Black Kite (*Milvus migrans parasitus*), a natural enemy for locusts, as a biological measure for locust outbreak control. Two types of experiments were done that included observed predation and experimental predation. It was observed, in the observed predation, that a higher number of locusts were found in the bird's stomach during the afternoon session (mean = 66) than during the morning session (mean = 21). The high peak observed during the afternoon session was also associated with the feeding of larvae of the migratory locust. The experimental predation results showed that almost 100 percent of the larval and 97 percent of the fledglings were fed on. The experimental predation results also showed that there was no preference for larvae or fledglings in the cage and that the bird fed on the different combinations equally. This study showed that the Black Kite birds can effectively control locust population in an outbreak when they are easy to predate on. However, there is a need to assess the population of birds in locust infested areas to determine if the bird population is enough to predate on a locust outbreak.

## Keywords

Integrated Pest Management, *Milvus migrans parasitus*, Locust, Madagascar, Avian Insectivory

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## 1. Introduction

Agriculture has been a very important sector in the economic development of countries for a very long time. The importance of agriculture lies in its ability to be a source of employment, raw material for industrial production, income to governments and most importantly as a source of food (Tiffen, 2003) [1]. In developing countries, the role of agriculture to poor families which spend less than a dollar a day is the only source of income and food; unlike in developed countries that have a variety of income generating options. Over 70 percent of poor families in developing countries are located in rural parts that have adequate land for crop production and pasture land for feeding livestock, but also spend their valuable working time in various agricultural activities (Hertel and Rosch, 2010) [2]. Despite the importance of agriculture to the rural poor population in developing countries, there have been various concerns in the ability of agriculture being reliable to the poor families to offer the required income and even food for the families. The poor families have consistently found agriculture to be unreliable because of low crop yields that are experienced every growing season. A lot of the farmers in developing countries often do not produce enough to feed their own families. The low crop yields in Madagascar, a poor African country, have been attributed to many factors that include loss of soil fertility, poor farming practices, climate change and use of unimproved crop varieties. However in South and Southwest regions of Madagascar, which are heavily infested by locusts, the most important factor leading to low yields is insects (Lecoq *et al.*, 2011) [3].

In Madagascar, the South and Southwest regions have for decades had locust outbreaks that have devastated crop fields (Lecoq *et al.*, 2011) [3]. The locust species dominant in this area are the red locust (*Nomadacris septemfasciata*) and the Migratory Locust (*Locusta migratoria capito*), both of which have geographically restricted outbreaks (African Development Bank, 2001 [4]; Magor *et al.*, 2008 [5]). The geographical restriction for the locusts is associated with the perfect environmental conditions in the region that allow them to go through the various stages of reproduction and also successfully survive. The solitarious and gregarious phases are the two main phases of locust population that represent the low population stage and the swarm population stage respectively (Sánchez-Zapata *et al.*, 2007) [6]. However, the gregarious phase is associated with crop destruction, because of the increased locust population that causes significant harm to crops and other types of vegetation. The behavior of locusts has led to them being categorized as pests because they are organisms that interfere with the goals and activities of humans (Lomer *et al.*, 2001) [7]. In the context of agricultural production, a pest can be defined as an organism which negatively influences the production of food and fiber (Shelton, AM, Badenes-Perez, 2006) [8].

Pest control has existed ever since humans started growing crops and rearing livestock as a source of food. In agricultural production, there is always a competition between humans and pests for limited resources required for growth of crops and survival of pests. In view of this, there has always been the need in agriculture production to control and mitigate the negative effects of pests through the use of various pest control practices. In Madagascar the use of chemicals as a control practice has been preferred and overused for a long period of time, but it is both expensive and leads to environmental pollution. Despite the focus on chemical control of locusts in Madagascar, there are three other options and include biological controls, cultural controls and physical controls. Biological controls generally include the use of predators and disease causing organisms for the control of pests (Kar *et al.*, 2012) [9]. A combination of these four categories of pest control is referred to as integrated pest management (IPM). The IPM approach is considered a better option because individual pest control initiatives do not have an effective outcome when compared to an integrated approach.

Many studies have been conducted to assess the beneficial direct interactions that exist between birds and plants (Meehan *et al.*, 2005) [10]. Birds are known to play important roles as pollinators (Meffe, 1998) [11], seed dispersers (Stiles, 2000) [12], seed predators (Castro *et al.*, 1999 [13], Howe and Brown, 1999 [14]), and herbivores (Noordhuis *et al.*, 2002) [15]. These direct interactions have been shown to affect plant population dynamics and community structure, as well as the evolution and expression of plant life histories and morphologies (Meehan *et al.*, 2005) [10]. Many bird species feed on locusts, but their ability to keep the locust population in check so as to avoid economic damage is not clearly known (Kirk *et al.*, 1996) [16]. *M. m. parasitus* is widely distributed in sub-Saharan Africa, Comoros, and Madagascar and has strong intra-continental movements (Cramp & Simmons, 1980 [17]; Fergusson-lees & Christie, 2001 [18]). It is a migratory bird that flies to Madagascar every year at around the time when the weather and food competition is suitable for its survival and reproduction. This migratory behavior brings the bird species in large numbers making them a menace to the locust pop-

ulations. Associated to the migratory behavior the bird occupies the study area (South and Southwest of Madagascar) in the period ranging from November to March, which is a time that coincides with high locust swarm development and propagation period. In this study, we considered the Black Kite (*Milvus migrans parasitus*) bird species in the area as a natural enemy for locusts; hence act as a biological preventive control method. However, questions existed on the locust feeding capability of the Black Kite (*Milvus migrans parasitus*) bird species to be considered as an effective biological preventive option that can form part of an IPM program. This paper aimed at determining the predation values from the Black Kite (*Milvus migrans parasitus*) bird species as a measure of effectiveness for locust outbreak preventive control. Furthermore, the study determined the predation values during both solitarious and gregarious phases.

## 2. Materials and Methods

### 2.1. Study Area

Madagascar is an African Island country that is located in the Indian Ocean and has a wide variety of biodiversity. This study was focused on the South and Southwest regions of Madagascar, which have a known record of locust outbreak problems. Just like the general biodiversity range of Madagascar, the South and Southwest regions have equally diverse vegetation that has mosaic vegetation units, which include Savannas, steppes, forest galleries, wastelands, and bushy areas. The study area is divided into three ecological zones based on the amount of rainfall received per year. Based on the annual rainfall amounts, the area is divided into three ecological units that support growth and development of locust swarms. The first ecological zone receives annual rainfall of 750 - 800 mm, the second zone records annual rainfall amount of 400 - 500 mm, and the third zone with the least average amount of rainfall receives 350 - 400 mm. These ecological zones are also associated with locust's solitarious and gregarious phases; with the highest rainfall receiving zone being the multiplication area and the other zones being multiplication transitional area and densing area respectively.

Two sampling stations were selected on the three ecological units associated with locust swarm development. The two stations were Bekily and Isoanala. Isoanala station located 23°50' South and 45°43' East, occupies an area of 3.75 km<sup>2</sup>. The Isoanala station was an open environment that consisted of anthropic mosaic polyculture fields of various plant species such as Acacia Tote has sp., Heath has *Indigofera* sp., *Heteropogon contortus* (Poaceae), *Cynodon dactylon* (Poaceae) *Hyphaena Shatan* (Arecaceae) and *Eucalyptus* sp. This station had several water stations and was favorable area for locust to propagate. The other station of Bekily are found between coordinates 23°21' to 24°05'14" South and 44°8'59" and 44°12'05" East. The station had have fertile soils that favor pasture growth and transhumance for farmers in surrounding areas. From the vegetation point of view, the Bekily had a dry bush land dominated by *Heteropogon contortus* grass species. The Bekily station was classified as the multiplication and gregarizing area.

### 2.2. Bird Sampling and Data Collection

There are over 40 bird species in the study area of which 11 are known locust predators. One of these bird species, the Black Kite (*Milvus migrans parasitus*) was selected because it is acknowledged as the main migratory insectivores. The Black Kite bird is a migratory bird and its largest population attendance in the months of November/December to June/July every year coincides with the locust outbreak periods. Furthermore the Black Kite bird is dominant in South and Southwest of Madagascar, and feeds on locusts larval and fledglings.

Observed predation (OP), 30 individuals' Black Kite birds (*Milvus migrans parasitus*) was sacrificed during this experimentation field works, the OP was done by examining stomach contents of hunted wild birds. It was based on determining the number of locust fed but also the development stage of the locust (whether larvae or adult). The stomach contents of birds were examined at different times of the day, and from different locations within the study under various locust events (spot, hopper band or swarm) either in remission or gregarious periods. During stomach content examination, the presence of non-digestible components such as head, abdomen, femur, and wings were used to identify the captured locusts. This method also provided information on the period of day when the bird's predation of locust was highest.

The experimental predation (EP) was done at Isoanala station and involved capturing breeds that were placed in semi-natural cages. The cages were made of wire mesh installed directly on the ground, and were 2 m × 1 m × 1.5 in size. In the cage, individual of Black Kite birds (*Milvus migrans parasitus*) was fed locusts of different

developmental stages (larvae and winged); the locusts were fed in three different combinations of only larvae, only adult locusts, and a combination of hoppers and adults. The locusts fed to the bird were counted before being placed in the cages and the remainders were also counted to know the number of locusts not fed on. The bird in the cage was fed every morning and the remainders were removed in the evening of each day. This captive-feeding method was used to determine predation of an individual bird species on locusts of different development stages.

### 2.3. Data Analysis

Studies of bird predation on locust were conducted from October 2012 to May 2013. Two types of experiments were done that included 1) experimental predation to estimate potential predation rate of birds on locusts; and 2) examination of captured bird stomach content. The results from these experiments were calculated by using descriptive statistics that included frequency, mean and standard deviation. The t-test was used to test the significance of the differences between the two group means, and the level of significance was set at 0.05.

## 3. Results and Discussion

### 3.1. Observed Predation

Stomach content data for the bird was collected by hunting the birds during two sessions of morning and afternoon (**Table 1**). The two sessions were separated to determine the time of day when the birds fed more.

**Table 1.** Black kite (*Milvus migrans parasitus*) bird stomach examination results.

Shooting times	Bird identity	Amount of locusts captured	Locust type	Vegetation
10:00 to 10:30 hrs	1M	22	Winged <i>Nomadacris</i>	Savannah
10:00 to 10:30 hrs	2M	19	Winged <i>Nomadacris</i>	Savannah
10:00 to 10:30 hrs	3M	11	Winged <i>Nomadacris</i>	Savannah
10:00 to 10:30 hrs	4M	13	Winged <i>Nomadacris</i>	Savannah
10:35 to 11:00 hrs	5M	15	Winged <i>Nomadacris</i>	Savannah
10:35 to 11:00 hrs	6M	17	Winged <i>Nomadacris</i>	Savannah
11:05 to 11:30 hrs	7M	10	<i>Nomadacris</i> larvae	Wasteland
11:05 to 11:30 hrs	8M	26	Winged <i>Nomadacris</i>	Savannah
11:35 to 12:00 hrs	9M	18	<i>Nomadacris</i> Larvae	Wasteland
11:35 to 12:00 hrs	10M	47	<i>Nomadacris</i> Larvae	Wasteland
11:35 to 12:00 hrs	11M	9	Winged <i>Nomadacris</i>	Dry forest
11:35 to 12:00 hrs	12M	11	Winged <i>Nomadacris</i>	Dry forest
11:35 to 12:00 hrs	13M	29	Winged <i>Nomadacris</i>	Savannah
11:35 to 12:00 hrs	14M	32	Winged <i>Nomadacris</i>	Savannah
11:35 to 12:00 hrs	15M	31	<i>Locusta</i> Larvae	Dry forests
13:00 to 14:00 hrs	1A	44	Swarm of <i>Nomadacris</i>	Savannah + Dry forests
13:00 to 14:00 hrs	2A	27	larvae of <i>Nomadacris</i>	Wasteland
14:00 to 15:00 hrs	3A	16	Swarm of <i>Nomadacris</i>	Wasteland
14:00 to 15:00 hrs	4A	19	Swarm of <i>Nomadacris</i>	Wasteland
15:00 to 15:30 hrs	5A	23	<i>Nomadacris</i> Larvae	Savannah
15:00 to 15:30 hrs	6A	25	<i>Nomadacris</i> Larvae	Savannah
15:00 to 15:30 hrs	7A	40	Big swarm of <i>Nomadacris</i>	Savannah + Dry forests
16:00 to 16:30 hrs	8A	215	<i>Locusta</i> Larval	<i>Heteropogon contortus</i>
16:00 to 16:30 hrs	9A	158	<i>Locusta</i> Larval	<i>Heteropogon contortus</i>
16:00 to 16:30 hrs	10A	104	<i>Locusta</i> Larval	<i>Heteropogon contortus</i>
16:00 to 16:30 hrs	11A	58	<i>Locusta</i> Larval	<i>Heteropogon contortus</i>
16:00 to 16:30 hrs	12A	43	<i>Locusta</i> Larval	<i>Heteropogon contortus</i>
16:30 to 17:30 hrs	13A	87	<i>Nomadacris</i> Larvae	Wasteland
16:30 to 17:30 hrs	14A	86	<i>Nomadacris</i> Larvae	Wasteland
16:30 to 17:30 hrs	15A	42	<i>Nomadacris</i> Larvae	Savannah + Dry forests

M: Morning period; A: Afternoon period

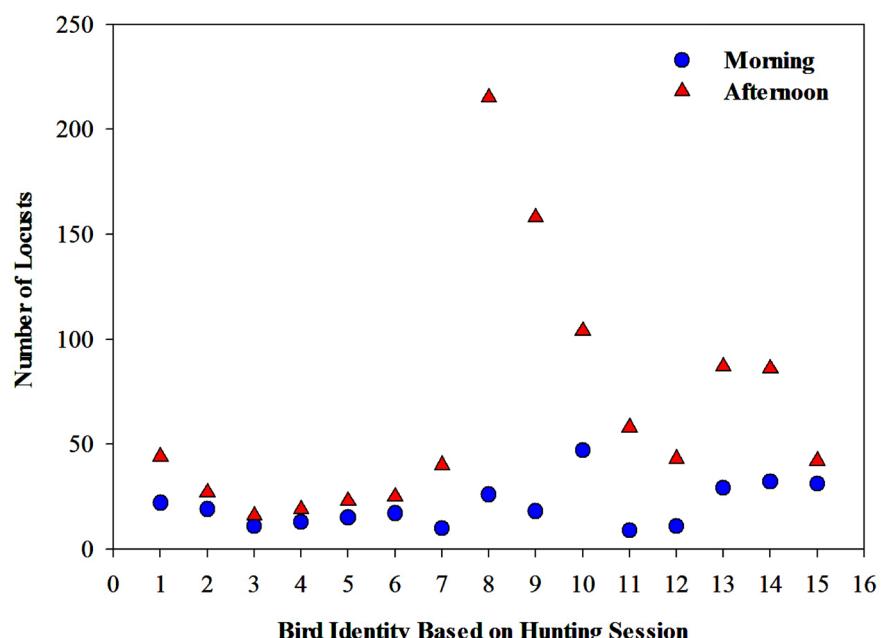
Furthermore, information on the hunting time period (in hours) was also collected to determine the actual time when the bird was at its feeding best. In this study, locusts referred to red locust (*Nomadacris septemfasciata*) and the Migratory Locust (*Locusta migratoria capito*); other types of grasshoppers and insects identified in the stomach were disregarded. The study also collected the locust type and stage of development that was found in the bird's stomach. The development identified were mostly of two groups winged adults and larvae locusts (**Table 1**). The vegetation identified during this study was composed of five types, which included Savannah, dry forests, *Heteropogon contortus*, a mixture of Savannah and Dry forests and Wasteland (abandoned land that was previously farm land). A total of 30 birds were hunted and stomach contents assessed, with 15 birds being hunted during each session of the day.

Between the morning and afternoon sessions, it was observed that a higher number of locusts were found in the bird's stomach during the afternoon session (**Figure 1**). The morning session trend was evenly spread out with small variations, while the afternoon session was constant in the early afternoon but increased in the late afternoon period. The trend specifically increased during sessions from 1600 hours to 1630 hours time period, and afterwards it went down; although not as low as the early afternoon trend (**Table 1**).

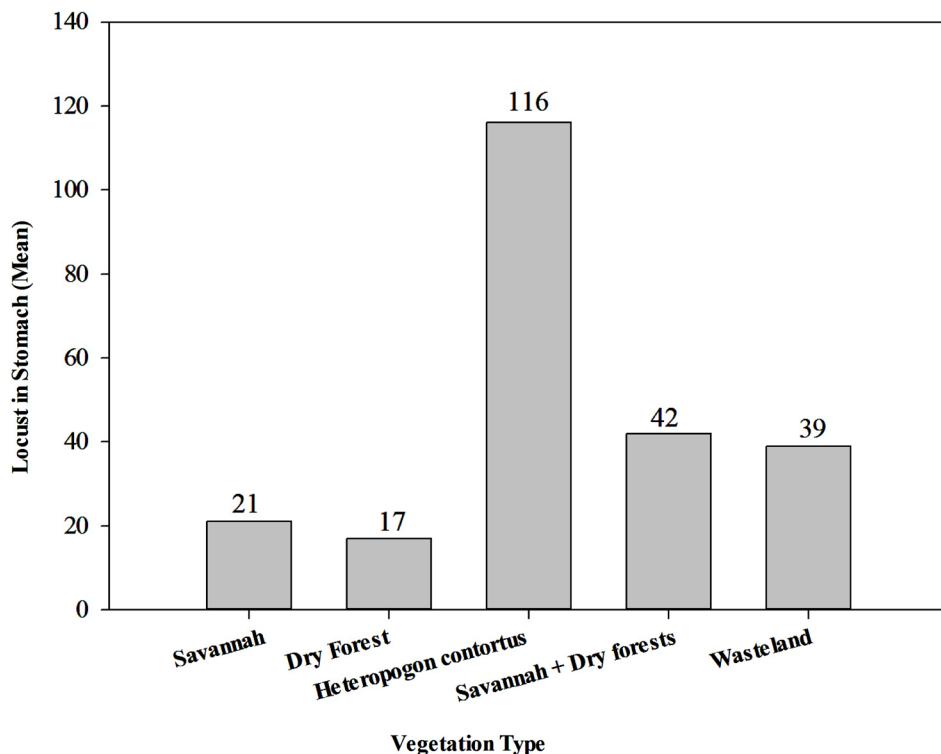
The high peak observed during the afternoon session was also associated with the feeding of Larvae of the Migratory Locust (*Locusta migratoria capito*) (**Table 1**). These might have been easy for the birds to capture and feed on as they were less mobile when compared to the winged adults that could fly away hence proving difficult to hunt. This observation may also be true for the birds captured during the morning session that had a lower count of locusts in their stomachs. The morning session had a large number of winged adult locusts captured (**Table 1**), which could be that the birds found it difficult to capture them; unlike the larvae locusts that were found in the bird's stomach during the late afternoon. Thus the Black Kite bird prefers to hunt on locusts that it can easily catch or that can be captured without wasting much energy.

The vegetation of the study area was also examined to determine if it influenced the bird's ability to capture the locusts (**Figure 2**). Birds captured feeding on locusts on the *Heteropogon contortus* grass had the highest average (mean = 116) of locust stomach contents. This vegetation also hosted the Larvae of the Migratory Locust, which was found to be the most fed on by the birds (**Table 1**). This indicated that the Larvae of the Migratory Locust preferred habiting in this vegetation, which is short grass that has a height of about 30 cm. This vegetation was also ideal for the bird to capture the locusts as the grass did not hide the larvae to limit the birds from capturing the prey.

The savannah + dry forests vegetation characterized by a large density of trees per hectare had birds with the highest average (mean = 42) of captured insects in the stomach (**Figure 2**). This vegetation was characterized by



**Figure 1.** Diagram showing amount of locusts in the bird's stomach during morning and afternoon hunting sessions.



**Figure 2.** Vegetation type and average of locusts found in birds stomach.

**Table 2.** Observed predation of the black kite (*Milvus migrans parasitus*) bird.

Calculation	Amount of locusts captured in morning	Amount of locusts captured in afternoon
Observed predation	21	66
Std deviation	11	57
Observations	15	15
Degrees of freedom	15	
t stat	-3.029	
P ( $T \leq t$ ) two-tail	0.008	
t critical two-tail	2.131	

both the adult and larva red locust (*Nomadacris septemfasciata*). There wasn't much difference between the savannah + dry forest vegetation and the wasteland vegetation that had a mean of 39 locusts found in the bird's stomach. The other vegetation types of big wooded savannah and dry forest followed with means of 21 and 17 locusts found in a bird. This led to the observation that areas that had high vegetative cover, such as with trees, were dominated by adult locusts and birds found it difficult to capture them under such vegetative cover.

The calculated OP for the locusts found in the stomach in total was 43 locusts per bird in a day, while in the morning and afternoon the OP's were 21 and 66 respectively (Table 2). The t-test statistic showed that there was a significant statistical difference ( $t(15) = -3.029, p = 0.008$ ) in the total number of locusts eaten in the morning and afternoon, which confirmed that the birds did not have a constant eating pattern. This calculation also confirmed that the birds fed on the locusts mostly in the afternoon than they did in the morning. This locust eating pattern was because of the vegetation type of where the bird had been hunted, which prevented the bird's flight ability in areas with large vegetative cover.

### 3.2. Experimental Predation

The experimental predation (EP) was done to determine the feeding potential of the Black Kite (*Milvus migrans parasitus*) bird on the locusts. This experiment was important as it took out any natural limiting factors that ex-

isted in the natural environment, in order to estimate how much the bird could predate on the locusts. During the experiment duration of 32 days, a total of 1079 larval and 2083 fledglings were fed to the caged birds. The results showed that almost 100 percent of the larval and 97 percent of the fledglings were fed on during this duration (**Table 3**). The EP for the larvae was calculated to be 77, while for the fledglings it was 65. The total EP

**Table 3.** Experimental predation of the black kite (*Milvus migrans parasitus*) bird.

Day	Amount of locusts caged		Amount of locusts eaten		Percent eaten	
	Larval	Fledglings	Larval	Fledglings	Larval	Fledglings
1	-	143	-	138	-	97
2	-	38	-	38	-	100
3	-	28	-	28	-	100
4	-	40	-	38	-	95
5	54	104	53	103	98	99
6	48	22	48	22	100	100
7	60	110	60	104	100	95
8	60	124	60	110	100	89
9	70	114	70	113	100	99
10	69	109	69	109	100	100
11	-	200	-	198	-	99
12	-	202	-	198	-	98
13	-	82	-	78	-	95
14	-	99	-	99	-	100
15	-	40	-	40	-	100
16	-	60	-	60	-	100
17	-	60	-	60	-	100
18	-	87	-	87	-	100
19	-	24	-	24	-	100
20	-	31	-	31	-	100
21	70	80	70	80	100	100
22	48	104	48	104	100	100
23	-	37	-	37	-	100
24	-	12	-	12	-	100
25	-	36	-	36	-	100
26	60	10	60	10	100	100
27	74	6	74	6	100	100
28	40	8	40	8	100	100
29	26	13	26	13	100	100
30	200	-	200	-	100	-
31	200	40	200	40	100	100
32	-	20	-	0	-	0
<b>Total</b>	<b>1079</b>	<b>2083</b>	<b>1078</b>	<b>2024</b>	<b>100</b>	<b>97</b>
<b>Expected predation</b>				Larval	77	
				Fledglings	65	
				Total	69	
				t-stat	0.681	
<b>t-test (larval vs fledglings)</b>				Degrees of freedom	25	
				p values (two-tail)	0.502	

was calculated to be even higher than that of fledglings at 69 locusts per bird, and most importantly was higher than the OP calculations that had a total of 43 locusts per bird. This was not surprising because the birds in the cages had no limiting environmental factors in the cage that could limit the bird's ability to hunt locusts. The environmental factor identified in this study was mainly the vegetation type, but others could include terrain, weather conditions such as precipitation limiting flight and competition with other insectivores. The EP results also showed that there was no preference for larvae or fledglings in the cage and that the bird's fed on the different combinations equally (**Table 3**).

#### 4. Discussion

Ecosystems are known for their roles in supporting their various members with resources for survival and other services that are crucial for individual organisms, but also their species as a whole. In the ecosystems, the food web is an interaction of organisms at different trophic levels that controls the performance of the general ecosystem, in terms of numbers. Two main approaches are central to the determination of the food web in an ecosystem and they include the top-down and bottom-up approaches (Hunter and Price, 1992 [19]; Polis *et al.*, 1997 [20]). The top-down approach is a type of mechanism that is controlled by the organisms up the food web, which are the main consumers; while the bottom-up approach is the opposite of its counterpart as it is resource driven, which means it is controlled by organisms that are at lower levels in the food chain (Mantyla *et al.*, 2011 [21]). These approaches have formed the basis for this study, where plants are the producers fed on by locusts that in turn are preyed on by insectivorous birds. However, locusts' swarms have been responsible for unsustainable consumption of plants, particularly crops in this case, to warrant the need for their predators in the ecosystem to control them. If an ecosystem is productive enough to facilitate the existence of vertebrate predators, the "ecosystem exploitation hypothesis" predicts that predators keep the population sizes of the notorious prey low, thus enabling plants to grow and reproduce (Oksanen and Oksanen, 2000) [22].

Observed predation (OP) of the Black Kite (*Milvus migrans parasitus*) bird was done by examining the bird's stomach contents to determine the number of locusts that were eaten. In performing this particular observation, this study predicted if the birds were able to enforce the ecosystem exploitation hypothesis in order to control gregarious phase of locusts. The results of the OP have shown the effect of vegetation on the ability of the Black Kite to feed on the locusts. Locust's reproduction involves laying of eggs in the soil and the larvae that don't have wings hop in vegetation that is close to the ground (Ambar, 2003 [23]; Massey *et al.*, 2007 [24]). The *Heretropogon contortus* vegetation hosted a large number of locust larvae that were highly fed on by the birds. Similarly the wastelands, which are abandoned agriculture lands that were undergoing natural vegetation re-growth, had a large number of locust larvae. However, in areas with taller vegetation, the adults' locust were dominant type found in the Black Kite bird stomach, which supported the observation that vegetation was associated to the size of locust found. The type of vegetation plays a role in attracting the birds to feed on insects that feed on it (Jones and Sieving, 2006) [25]. It was normal to observe in our study that birds caught in savannah and partly dry forest had a high number of locusts in their stomachs, maybe because the birds were attracted to this area.

Care in interpreting the results of stomach contents in birds was considered in this study, specifically on the number of adults and hoppers. In terms of numbers, the adult locusts were found in fewer numbers because they are larger in size hence the birds had to capture more hoppers than the adult locusts. This led to the experimental predation to assess if the Black Kite preferred eating hoppers or the adult locusts. A total of 1079 larval and 2083 fledglings were fed to the caged birds. The results showed that almost 100 percent of the larval and 97 percent of the fledglings were fed on during this duration. The EP for the larvae was calculated to be 77, while for the fledglings it was 65. Most avian species have opportunistic traits in their feeding habits, switching food types to take advantage of readily available food sources. For instance, during an insect outbreak in a Polish forest, predation of passerine nests declined, as predators switched to feeding on caterpillars (Tomialojc and Wesolowski, 1990) [26]. This indicates that the Black Kite bird generally feeds on the readily available locust that can easily be caught by the bird. Since the adult locusts are difficult to capture than the hoppers, then it would be no surprise that the fledglings were mostly captured in both experiments.

This study showed that the Black Kite birds can effectively control locust population in an outbreak when they are easy to predate on. Furthermore, the birds can be used as part of an IPM approach that can be used with other strategies. Despite the positive observation of this study, there is a need to assess the population of birds in locust infested areas to determine if the bird population is enough to predate on a locust outbreak and make an

effective contribution to an integrated locust control approach. Such an assessment would correlate between the population of Black Kite and the role they can play in an IPM initiative. The role of parasites and predators, as a factor in the regulation of locust populations, has been thoroughly investigated and widely debated in the literature (Kirk *et al.*, 1996 [16]; Szabo, 2005 [27]; Fildes *et al.*, 2006 [28]; Whelan *et al.*, 2008 [29]). The effects of predators and parasites are suggested to be modified by environmental conditions and by the stage of the outbreak (Wenny *et al.*, 2011) [30]. Few natural enemies are associated with locust populations during the build-up phase, as parasites and predators depend on stable or declining populations (Lomer *et al.*, 1999) [31].

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