i. Preface

This study has been possible through the academic and technical support of the Department of Zoology and Wildlife Conservation of the University of Dar es Salaam (UDSM) and Norwegian University of Science and Technology (NTNU). Thanks are due to the Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA) and the Ministry of Natural resources and Tourism (MNRT) for their permission to conduct research in Serengeti. Special thanks to the World Bank sponsored Lower Kihansi Environmental Management Project (LKEMP) for funding this study.

I am highly indebted to my main academic supervisor Professor Eivin Røskaft who inspired, advised and guided me throughout the period of my study. Thanks are due to my second supervisor, Dr. Charles Mlingwa for his guidance especially in the development of my PhD study proposal. I am also grateful to my co-authors Tomas Holmern, Sigbjørn Stokke, Bård Stokke, Børge Moe and Grayson Mwakalebe. I am thankful to the NTNU's Biology Department staff including Tove Tronvold, Jasenka Zvizdic, Ingunn Yttersian, Åsa Krøkje, Lisbeth Anne, Hans Jakob Jakobsen and Inger for their support.

I am highly indebted to the TAWIRI staff for their hospitality and assistance. I would also like to thank people working with Lion, Hyena, Carnivore disease projects and Frankfurt Zoological Society for their cooperation during my stay in Serengeti. Thanks are also due to John Kaaya, Asanterabi Lowassa, Hassan Nkya and Honory Maliti for their helpful relevant information on my study. I am grateful to Grayson Mwakalebe, Noel Massawe, Wilfred Marealle, Joshua Kabondo, Elias Kalumbwa and Onesmo Mwakabejela for their excellent field assistance. Special thanks to Regina Maliki and Jane Kabondo for taking care of me during my stay in Serengeti. I would also like to extend my appreciations to Emmanuel Gereta, Julius Nyahongo, Vedasto Ndibalema, Claudia Melis, Mark Keith, Craig Jackson, Trine Hay Setsaas, Hassan Shombe, Jafari Kideghesho and Iddi Mfunda for fruitful discussions and comments. A special thank to Ragna Sortland for being my field associate and for sharing many thoughts and ideas about ostrich research. My thanks also go to Nina Bjørken, Håkan Hytteborn, Brita Hytteborn, Berit Røskaft and Graciela Rusch for the company, social activities and sometimes assistance in the field in Serengeti that have served as an important source of inspiration and motivation.

Finally, many thanks to my mother, Dorica Magige for being a good mother and for taking care of my kids, Brian and Dorica, while abroad for my studies. Special thanks to my beloved husband, Agathon Kipandula and my whole family for moral support, patience and endurance of my absence.

Trondheim 2007 *Flora Magige*

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ii. List of papers

This thesis is based on the following five papers:

I. Magige, F.J., Stokke, B.G., Sortland, R. Røskaft, E. (Submitted). Breeding biology of ostriches (*Struthio camelus*) in the Serengeti ecosystem.

II. Magige, F.J., Moe, B., Røskaft, E., 2008. The white colour of the ostrich (*Struthio camelus*) egg is a trade-off between predation and overheating. Journal of Ornithology DOI 10.1007/s10336-088-0273-2

III. Magige, F.J., Stokke, B.G., Røskaft, E., (Submitted). Do ostriches (*Struthio camelus*) recognise their own eggs?

IV. Magige, F.J., Mwakalebe, G., Røskaft, E., (Submitted). Sex ratios and group dynamics in ostriches (*Struthio camelus*) in the Serengeti ecosystem, Tanzania.

V. Magige, F.J., Holmern, T., Stokke, S., Mlingwa, C., Røskaft, E., (Manuscript). Does illegal hunting affect density and behaviour of African grassland bird species? A case study on ostrich.

iii. Summary

This thesis focuses on the ecology and behaviour of the ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania. Ostrich is a large, flightless, cursorial, communal breeding bird, endemic to a variety of open habitat types of Africa. It is classified as ‘Least Concern’ under the IUCN Red List. Nevertheless, wild ostrich populations have been declining and considered ecologically extinct in most parts of western and northern Africa due to habitat loss, egg collection and illegal hunting.

The first section of this thesis (Paper I) investigates the effect of topography, rainfall and predation on breeding success of ostriches in the Serengeti ecosystem. Differences in the altitude and amount of rainfall in the ecosystem affect the breeding success of the ostriches. In the low altitude western area, ostriches laid eggs earlier than in the high altitude eastern area. The differences could be attributed to the rainfall and food gradients, which increase towards western area. In addition, high breeding success observed in the western area could be atrributed to the vegetation type that conceals the nests.

Following this section, the Paper II and III of the thesis examines the possible biological reasons why ostrich eggs are white in colour and whether female ostriches are able to recognise their own eggs when confronted by intraspecific brood parasitism. During the egg laying period, ostriches leave their eggs unattended for approximately two weeks before the incubation start. In this period the eggs are exposed to high levels of predation due to their conspicuousness. The reasoning of the eggs being white has been attributed to reduce and overcome heat stress. The temperature experiments on painted and control eggs revealed that the inner temperature of the brown painted eggs reached lethal temperatures. Developing embryos would die, should ostrich eggs have been brown in colour. White painted and control eggs were below the threshold temperature where the embryo mortality starts to increase, indicating that white eggs prevents overheating. However, white colour increases predation risks due to high visibility. In addition, following communal nesting behaviour of ostriches, nests commonly end up with many more eggs than can be incubated. Since the ostrich can only incubate less than 20 eggs, at the onset of incubation the ‘major’ female (the first female to lay the egg in the nest and subsequently undertakes guarding and incubation), ejects some of the eggs. The ejected eggs are presumed to belong to the ‘minor’ females (females that subsequently

lay eggs on the same nest). There was no clear pattern of movement of eggs in the nests, and ejection of eggs was random. Ejected eggs that were experimentally put back in the nest were never ejected again. Spectorophotometric study compared inner central eggs in the nest and ejected eggs in colour variance. Results revealed no significant difference in colour between the eggs, indicating that ostriches do not recognise their own eggs but eject eggs randomly.

The next section of the study (Paper IV) investigates spatio-temporal sex ratio and group dynamics in areas with different conservation status (i.e. national park and partially protected areas). In accordance with previous studies, adult sex ratio (female/female+male) was found to be female biased. There was spatial and temporal variation in sex ratio, with a highly female skewed sex ratio inside the national park, compared to the partially protected areas, and dry season compared to wet season. The probable reason could be differential mortality between sexes following males solitarily and territorial behaviour. Furthermore, adult sex ratio was found to be influenced by group size, where sex ratio increased with group size. However, there was no significant difference in group size between national park and partially protected areas or between habitat types. Group sizes also varied with seasons. Larger group sizes were observed in wet seasons, this could be associated with increased quality and quantity of food and natal recruitments towards the end of dry season. Single males were observed more frequently during dry season, compared to during the wet season. This can be accredited to the breeding season being in the dry season. Group composition also varied with group size, and members of each group consisted of a large number of females i.e. sex ratio increased with group size.

The final section of the thesis (Paper V) evaluates the effects of human disturbances on ostrich behaviour. Illegal hunting is widely spread in partially protected areas, mainly for subsistence and/or commercial purposes. Ostrich densities were not significantly different between the national park and partially protected areas. However, in the partially protected areas, birds were more wary with higher flight initiation distance (distance from an approaching threat at which a prey animal moves away/takes flight) compared to the national park upon human approach. This is an indicator of human disturbance in the partially protected areas.

High ostrich breeding success in the western area of the Serengeti indicates existence of metapopulations, where this area can be regarded as a ‘source’. Protecting the western corridor will allow free migration of birds since the eastern area appears to have high predation rate on nests. However, future studies should investigate the effects of climatic changes on the reproductive performance of ostriches. On the other hand rampant illegal hunting practised in the partially protected areas affect ostrich behaviour, which could ultimately lead to compromised foraging and reproduction. Wildlife managers therefore need to use flight initiation distance to identify set back zones - areas beyond which species are not disturbed by humans.

1. Introduction

Africa is a continent richly endowed with biodiversity. Her treasures of diverse life forms have been a source of interest since the advent of European explorers in the nineteenth century (Western 2003). The continent holds over 2,000 bird species, 20% of the planet's total, of which nine-tenths are African endemics and the rest are winter visitors from the Palaearctic (Dowsett and Forbes-Watson 1993).

Africa's 800 million people have co-existed with birds and other biodiversity for centuries largely using indigenous knowledge to maintain the ecological balance. However, the continent's biodiversity is threatened by increasing human activities that are deleterious to the environment for example logging, illegal hunting, agricultural expansion, and large scale development projects (Campbell and Hofer 1995; Hofer et al. 1996; Sinclair et al. 2002). Such activities have indirect impact on the biodiversity through habitat loss and fragmentation, overexploitation, habitat modification and species introduction which collectively lead to mass species extinctions (Meffe and Carroll 1997).

Creation of protected areas has long been referred to as the most feasible strategy of ensuring that neither over-harvesting nor habitat loss deplete wildlife resources (Chape et al. 2003). Protected areas around the world are receiving increased focus due to the rising awareness of their enormous contribution to conserving biodiversity. Nevertheless, preserving natural wildlife of the world today is a huge challenge, considering the growth rate of the human population and degradation of the animals' natural habitats (Sinclair 1995; Pelkey et al. 2000).

Approximately 39.8% of the total land of Tanzania is considered to be protected, in which partially protected areas (IUCN category ≤ IV) occupy two third of the area (Fig. 1) (Chape et al. 2003; WRI 2005). In recent years, human population has increased significantly in areas adjacent to protected areas and hence cause pressure on the wildlife through illegal hunting (Herremanns 1998; Caro 1999b; Loibooki et al. 2002; Kideghesho 2006). Therefore, one of the most immediate and pressing needs is to maintain grasslands that are large enough to provide a critical habitat for grassland birds, which have shown consistent declines in recent decades (Herremans 1998; Sinclair et al 2002).

The Serengeti ecosystem in Tanzania holds one of the largest natural grasslands of the world which are renowned for their large herds of mammals.

However, the bird community structure of these grasslands has been inadequately studied (Gottschalk et al. 2007).

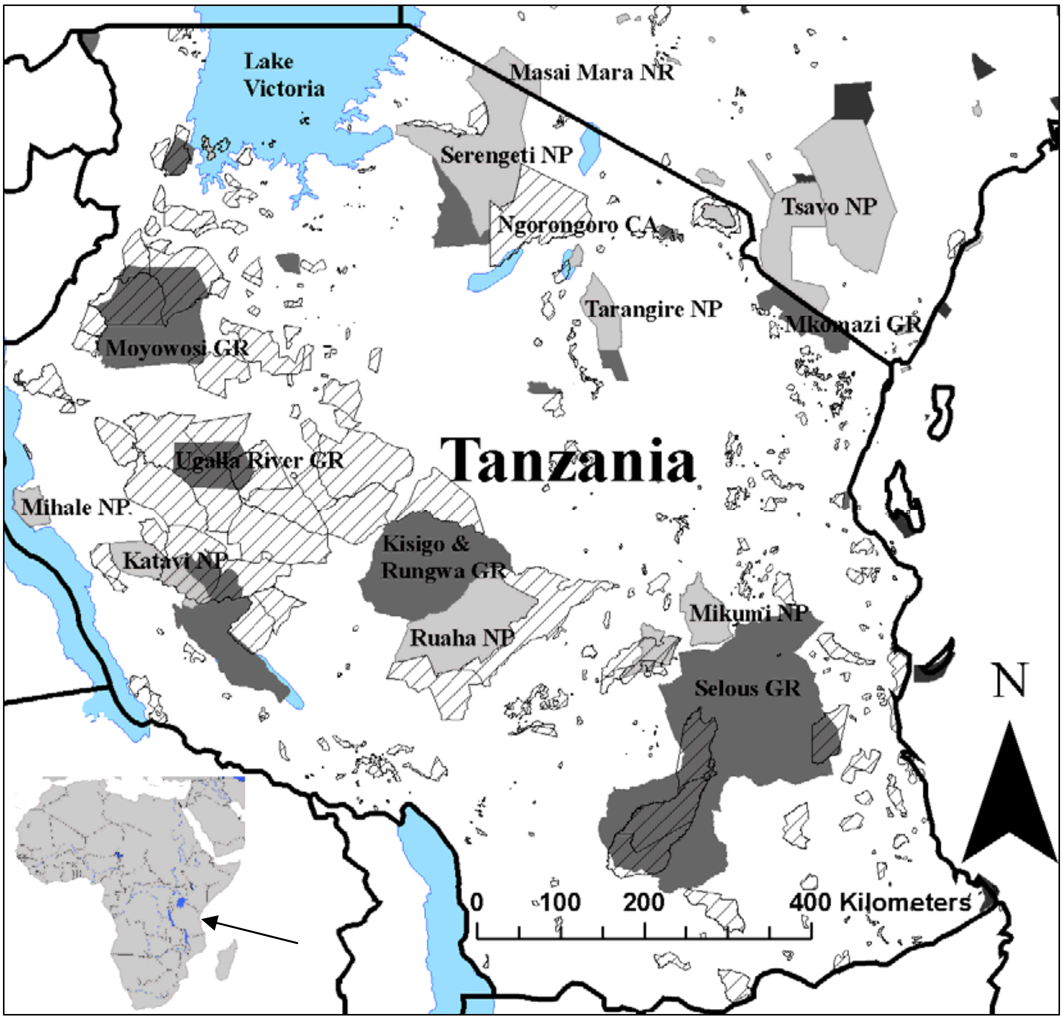

Fig. 1. Map showing the distribution of the different protected areas in Tanzania. Light grey areas are National Parks (NP), dark grey areas are Game Reserves (GR) and hatched areas are Game Controlled Areas, Forest Reserves, Open Areas and “other” partially protected areas. Arrow shows the location of Tanzania in Africa (taken from UNEP-WCMC 2005).

Serengeti ecosystem is classified as a potential important bird area and as an endemic bird area particularly because of its grassland bird community (Stattersfield et al. 1998; Fishpool and Evans 2001). Since the ecosystem is subject to relatively little human disturbance it offers a remarkable opportunity to study the grassland bird communities with respect to different topography, levels of conservation status (i.e. national parks versus partially protected areas) and habitat types.

Ostrich (*Struthio camelus massaicus*) is one of the grassland bird species selected for this study. Most comprehensive published studies of wild ostriches are mainly to aspects of ostrich farming, anatomy, physiology and pathology (Siegfried and Frost 1974; Bezuidenhout 1986; Brown et al. 1993; Degen et al. 1994; Deeming 1995). Until now, few studies have been conducted on the breeding and ecology of ostriches (e.g. South West Africa (Sauer and Sauer 1966); Zimbabwe (Jarvis et al. 1985); and Kenya (Bertram 1992). Thus, no study has been carried out on the breeding and behaviour of ostriches in the Serengeti Ecosystem. This thesis presents results obtained on the breeding biology of ostriches with focus on the laying dates, effect of large predators on reproductive success, effect of temperature on eggs, incubation behaviour, sex ratio and group dynamics. It also examined the influence of human disturbance on the ostrich behaviour.

1.1 Breeding biology and behaviour ecology

Ostriches are known to breed during the dry season starting from July to October (Brown and Britton 1980), with a strong selection pressure to lay eggs at the proper time (van Noordwijk et al. 1995; Dunn 2004; Visser and Both 2005; Drent 2006). Evolution generally has adjusted the timing of avian breeding seasons to maximize the number of young produced (Ehrlich et al. 1988). However, over the last decades the phenology (the timing of seasonal activities such as date of emergence of leaves and flowers, timing of breeding) (Walther et. al. 2002) of animal species has advanced and that these shifts are related to climate change (Walther et al. 2002; Dunn 2004). This climatic change associated with increased spring temperatures, has led to mismatch in the timing of egg laying relative to the availability of food in many but not all bird species (Drent 2006). As a result some species are unable to track the advancing phenology of the vegetation and/or prey abundance (Visser et al. 1998; Sanz et al. 2003).

Breeding adults, growing nestling and juveniles require abundant food supply (Williams 1966). Food shortage leads to delayed laying and therefore the offspring will not benefit fully from food abundance as postulated by Perrins (1970). Therefore, cues such as food availability affect timing of the onset and the end of reproduction (Goldman et. al. 2004). In the Serengeti ecosystem altitudinal and rainfall heterogeneity may have an effect on the breeding of ostriches. Low altitude areas receive more rain than higher altitude areas. It is hypothesized that ostriches in the low altitude western area will have an advanced laying date due to rich food supply that builds up the reproductive cycle towards the end of the dry season, than populations of the eastern area would. Ostrich nests are well camouflaged during laying period although experience high predation risk from Spotted hyenas (*Crocuta crocuta*), Egyptian vultures (*Neophron percnopterus*) and lions (*Panthera leo*) (Bertram 1992). Nests are located visually or other cues may be used such as observing parental activities (Collias and Collias 1984; Martin et al. 2000). Nest predation may be associated with occurrence of ‘singletons’ (single eggs laid randomly outside the nest without parental care). Predator threats disturb females that are laying and may consequently lay singleton anywhere without a nest while escaping (Sauer and Sauer 1966). It is therefore hypothesized that, areas with high densities of predators, will have high frequency of singletons due to disturbances upon laying females.

When breeding season starts, the territorial male prepares several scrapes (sufficiently deep nesting depressions in the ground) within its territory. The first female which subsequently selects one of these scrapes and lays eggs is considered a ‘major’ female, whereas the females that subsequently lay are considered ‘minor’ females (Sauer and Sauer 1966; Bertram 1992). Such a communal laying system is regarded as intraspecific brood parasitism, and has been reported to occur mainly among colonially breeding birds (Yom-Tov 2001), precocial birds (Yom-Tov 1980; 2001; Bertram 1992) and other ratite species (Coddington and Cockburn 1995).

Most ground nesters have pigmented eggs (Lack 1958, 1968). Surprisingly ostriches lay creamy white eggs that are left unattended for almost two weeks before the start of incubation (Bertram and Burger 1981; Bertram 1992). Previous works on avian egg pigmentation suggest that white eggs may be an adaption in dimly lit nests (Lack 1958; Kilner 2006). Egg crypsis is commonly associated with ground nesting birds as an antipredator strategy (Lyold et al. 2000; Sanchez et al. 2004). Even though egg pigmentation reduces predation risk, generally a pigmented surface absorbs more radiant heat than white surfaces (Montevecchi 1976; Bertram and Burger 1981; Kilner 2006). Therefore, it is hypothesized that birds that lay eggs in an exposed nest on the ground must trade-off the risk of predation and overheating.

At the onset of incubation both males and females attend the nest alternately with the male sitting on the nest overnight (Sauer and Sauer 1966; Bertram 1992). Nests can have as many as 40 eggs (Bertram 1979). Since ostriches can only incubate up to about 20 eggs (Bertram 1979; Kimwele and Graves 2003), host defence against minor female parasitism is through recognition and rejection of parasitic eggs. Excess eggs are ejected out of the nest by the major female while avoiding pushing out her own eggs basing on the size, shape and surface texture (Bertram 1979; 1992). Recently, spectrophotometric procedures have been invented and are now widely used in investigating features of avian eggs (e.g. Starling et al. 2006; Avilés et al. 2006, 2007; Cherry et al. 2007a; b). In this regard, ostrich eggs even though white in colour, might vary in reflectance which aid the major female to eject excess foreign eggs in her nest. An assumption is that there is low intraclutch variation and she is therefore able to recognise alien eggs basing on differences in reflectance.

1.2 Sex ratio and group dynamics

Given a generally balanced offspring sex ratio (Fisher 1930), little is known about adult sex ratios commonly defined as the sex ratios of breeding adults, but in practise commonly measured as the sex ratio of all independent non-juvenile individuals (Mayr 1939). Variations exists in adult sex ratio, which can be greatly skewed towards either males or females (though generally males) and the imbalance might be associated with a number of physiological or behavioural traits (Mayr 1939; Mcllhenny 1940). Skewed sex ratios remain frequently proposed though rarely quantified (Clutton-Brock and Parker 1992; Gerber 2006). A better understanding of the adult sex ratio and the relationship with demography, behaviour and population persistence may contribute a great deal to many areas of research. Behaviours such as polygyny, mate-guarding and communal breeding have frequently been linked to skewed adult sex ratio, and indeed may have evolved in response to them (Murray 1991). Previous studies on ostriches have indicated a female biased sex ratio in the national parks (Hurxthal 1979; Bertram 1992). However, no comparative study have been undertaken to investigate potential difference between national parks and partially protected areas. The current study provided an opportunity to examine the differences in ostrich sex ratios between the two areas, and the opportunity to investigate relationship between sex ratio and group sizes.

Living in groups has been found to be associated with increased vigilance and reduced individual vulnerability (Bertram 1980; Elgar 1989; Fernandez et al. 2003). However, the presence of a group-size effect is debatable as relatively few studies supporting the group-size effect have controlled for potentially confounding factors that affect the individual vigilance level, e.g. group composition or quality of intra-group social relationship (Quenette 1990; Blumstein et al. 1999; Beauchamp 2001, 2003).

Ostriches usually spend most of their time solitarily, although formation and splitting of groups occur frequently, with males adopting a territorial behaviour particularly during the breeding season (Roberts et al. 1970; Bertram 1992; Paper IV). Females usually form associations with other females and slightly more likely than not be accompanied by males (Bertram 1992). Single individuals attract more predation attempts than large groups when their heads are down (Bertram 1980, 1992). Males are particularly prone to predation (Bertram 1992), and since predation has been found to regulate populations (Sinclair et al. 2000; Sinclair et al. 2003), demographic pattern may change in terms of skewed sex ratios in areas with high predation pressures.

1.3 Human disturbance on ostriches

Although only predation causes direct mortality, both predation risk and human disturbances potentially affect population dynamics indirectly by altering an individual's investment in anti-predator behaviour (Gill and Sutherland 2000). For example illegal hunting has been severely affecting the ostrich populations (Bertram 1992; Thiollay 2006 a, b). Once widespread on open plains in low-rainfall areas of Africa (Brown et al. 1982), ostriches are becoming increasingly scarce throughout their ranges (CITES 2005), due to hunting, habitat destruction and foraging competition. Ostrich eggs, skin and feathers have long been prized (Bertram 1992; Ostrowski et al. 2001). Such human disturbances have been found to influence species population dynamics and behaviour (Frid and Dill 2002; Ikuta and Blumstein 2003).

Vulnerability of wildlife to disturbances depends on their exposure to human threats and biological characters that may cause some species to be more threatened with extinction than others. Body size influences vulnerability (Blumstein 2006) as well as a species' extinction risk (Cardillo 2003; Cardillo et al. 2005). Larger body size is a correlate of extinction risk (Gaston and Blackburn 1995) and therefore, larger bodied species are more wary and initiate flight at greater distances than smaller species (Fernández-Juricic et al. 2002; Blumstein et al. 2005; Blumstein 2006). For example, high hunting pressure in partially protected areas of the Serengeti Ecosystem

(Loibooki et al. 2002), may create greater wariness, use of suborptimal areas and exposure to predation and therefore a reduced reproductive success of the species (Blumstein et al. 2005).

2. Aims of the thesis

The aim of this thesis was to evaluate the breeding biology and behavioural ecology of ostriches in the Serengeti ecosystem. The thesis is divided into two parts. The first part of this thesis (Paper I-III) investigates the breeding biology and incubation behaviour of ostriches. The second part (Paper IV-V) evaluates demographic patterns as well as the consequences of human disturbance on ostrich densities and behaviour.

Objectives

The thesis focused on the following objectives:

- Evaluation of the effects of altitude and rainfall heterogeneity on the ostrich laying dates and breeding success.
- Investigation of why ostrich eggs are white in colour
- Investigation of whether ostrich recognises its own eggs and eject foreign eggs during incubation period.
- Investigation of ostrich sex ratios and group dynamics between the national park and partially protected areas.
- Evaluation of the consequences of illegal hunting on the ostrich density and behaviour.

3. Methods

3.1 Study area

Serengeti-Mara Ecosystem is located on the border of Tanzania and Kenya (1° and 3° S and 34° and 36° E), with a total area of approximately 25,000 km^2 (Fig. 2). The ecosystem supports not only the largest herds of migrating ungulates but also one of the highest concentrations of birds and large predators. It is one of the largest animals' sanctuaries in the world. The ecosystem is composed of networks of protected areas including the famous Serengeti National Park (14,763 km^2), Ngorongoro Conservation Area (8,288 km^2), Maswa (2,200 km^2), Ikorongo (563 km^2) and Grumeti Game Reserves (416 km^2), Ikoma Open Area (600 km^2), Loliondo Game

Controlled Area (4,000 km^2), and the Masai Mara Game Reserve (1,368 km^2, in Kenya). The Serengeti Ecosystem lies between the shores of Lake Victoria in the west, Lake Eyasi in the south, and the Great Rift Valley to the east. The Serengeti National Park was established in 1951, proposed as a World Heritage Site by UNESCO in 1972, and as a Biosphere Reserve, along with Ngorongoro Conservation Area in 1981.

The study was mainly conducted in the Serengeti National Park, adjacent Ikorongo and Grumeti Game Reserves and Ikoma Open Area. The ecosystem is part of the high interior plateau of East Africa. It slopes from its highest part (1850 m) on the eastern plains toward Speke Gulf (920 m) (Sinclair 1995). The temperature ranges from around 14°C at night to around 28°C during the day with a relatively constant annual mean of 21°C. Rainfall is mainly restricted to the wet season from November to May and typically falls in a bimodal pattern. The short rainy season is between November to January and the long rainy season is between March to May when there is heavy downpour (Norton-Griffiths et al. 1975). However, the rains can fuse into one long period, particularly in the north, or the short rains can fail entirely especially in the southeast (Sinclair 1995). The mean annual rainfall varies from 800 mm in the eastern to 1,050 mm in the northern part of the study area (Campbell and Hofer 1995). The vegetation varies from open short and long grass plains in the south, an extensive block of acacia savannah woodland in the centre. Hilly, wooded grassland in the north, and the western corridor which extends up to the edge of Lake Victoria is a region of wooded savannah and woodland. A unique combination of diverse habitats supports more than 30 species of large herbivores and nearly 500 species of birds.

Most of the Serengeti ecosystem in early 20th century was occupied by scattered human population who were mostly hunters and pastoralists. Recently, the growing human population has impacted the ecosystem through various human activities such as illegal hunting, infrastructural development, agriculture, livestock keeping, and pole cutting. Illegal hunting is commonly practised in villages adjacent to the western part of the Serengeti National Park, whereas the Maasai pastoralists to the east consume mainly livestock meat. Illegal hunting has been driven by the need to increase food supply, cash income and fulfil cultural and social needs (Loibooki et al. 2002; Kaltenborn et al. 2005).

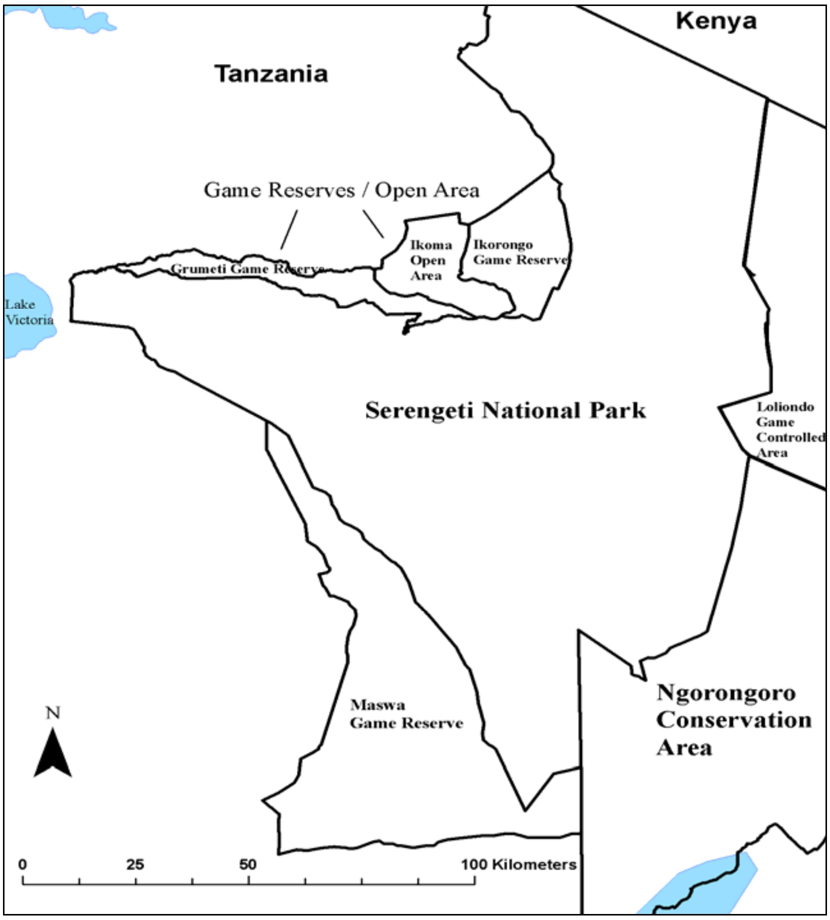

Fig. 2. Map of the Serengeti Ecosystem showing Serengeti National Park, and adjacent partially protected areas.

3.2 Study species

Ostrich is the largest flightless, herbivorous bird, found in a variety of open habitat types (Brown et al. 1982). It avoids areas of thick bush or of heavy tree cover. Adult male ostriches stand between 2.1 and 2.7 metres high (Cramp and Simmons 1980). They weigh up to approximately 145 kg but females are slightly smaller and lighter (Bertram 1992). The adult male's body plumage is jet black, with an exception of white plumage on its wings and tail. The female's feathers are of uniform earthy brown-gray colour. Much of the body is devoid of feathers, particularly the long neck, the whole of the legs and patches on the underside of the body (Bertram 1992). They are distinctive in their appearance, with a long neck and legs and the ability to run at speeds of about 60-70 km/h (Brown et al. 1982), with strides of up to 8.5 m (Smit

1963). Ostriches have the largest eyes of any terrestrial animal, with a diameter of 50mm (Hurxthal 1979).

The ostrich is the only living species of its family Struthionidae and order Struthioniformes that survived to the present day with four extant subspecies on the African continent (Sauer and Sauer 1966). The Masai ostrich (*S. c. masaicus*), Somali ostrich (*S. c. molybdophanes*), North African ostrich *(S. c. camelus)* and South African ostrich (*S. c. australis*) (Fig. 3). The Arabian ostrich *(S. c. syriacus)* became extinct in the mid 20th century (Bertram 1992). Although the distribution of the ostrich has severely declined over the past decades, they are categorised as 'Least Concern' in the International Union for Conservation of Nature (IUCN) Red List (IUCN 2006).

Ostriches reach sexual maturity after two to three years, and breeding seasons vary with locality, but in east Africa ostriches mainly nest in the dry season (Brown and Britton 1980; Perrins 2003). Males are territorial particularly during breeding season with territories averaged around 16 km^2. Females travel over considerably larger areas than males, with range approximately 26 km^2 (Bertram 1992).

A female ostrich lays up to a dozen eggs, laying on alternate days (Bertram 1992). Incubation time lasts about 40 days. Males and females take turns, but the males usually do the "night shift" although this rule is not invariable (Sauer and Sauer 1966; Bertram 1992). Ostrich eggs are the biggest bird eggs in the animal world. Nevertheless, in proportion to the size and weight of a female ostrich, they are the smallest eggs of any species (Perrins 2003). An average egg weighs about 1.5 kg, creamy white in colour and about 2 mm shell thickness (Bertram 1992).

Generally, ostriches occur naturally on the savannas and semi-deserts. Their distribution is almost independent of water as they can withstand a considerable degree of dehydration (Cloudsley-Thompson and Mohamed 1967). Due to their size and preference of more open habitat types, they are regularly encountered in wildlife areas where they frequently associate with other herbivorous animals. The main predators of ostriches include lions (*Panthera lion*) and hyenas (*Crocuta crocuta*) (Kruuk 1972; Schaller 1972; Bertram 1992), although cheetahs (*Acinonyx jubatus)*, leopards (*Panthera pardus)* and wild dogs (*Lycaon pictus*) can also be a threat (Sinclair et al. 2003).

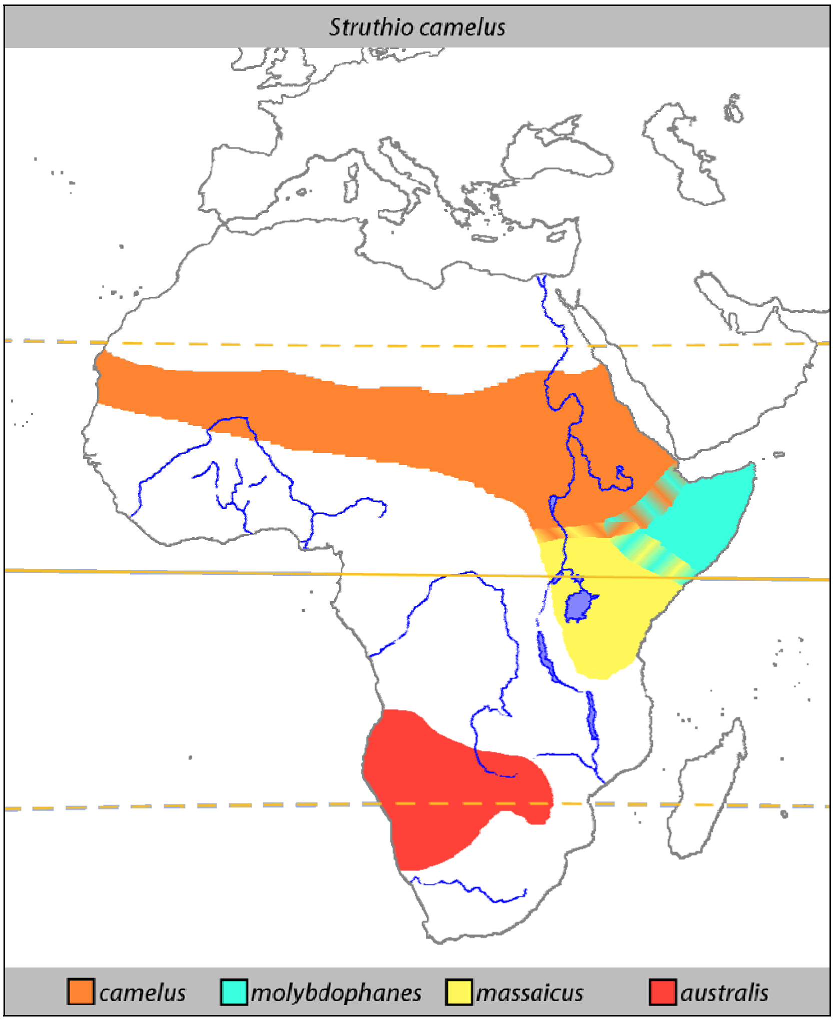

Fig. 3. Present distribution of ostrich subspecies in Africa. Derived from http://en.wikipedia.org/wiki/Ostrich

3.3 Data collection

The study was conducted between 2003 and 2006. Field data on the nesting and nesting success was collected between 2005 and 2006 (Paper I). Temperature experiments and visibility study on the painted and control (unpainted) ostrich eggs was conducted in December 2006 (Paper II), while investigation on whether major females recognise their own eggs in communal nests was done in the dry season 2006 (Paper III). We also collected data on the ostrich sex ratio and group dynamics between 2005 and 2006 (Paper IV). From 2004 to 2005 we collected data for density estimates of ostriches along the established transects both in the national park and partially protected areas (Paper V). In the late 2003 and early 2006 we collected data on ostrich flight behaviour (Paper V) and in the mid of 2006 we also administered questionnaires to the local people surrounding the Serengeti National Park to assess illegal hunting and uses of bird products.

4. Summary of results

4.1 *Paper I*

Ostrich (Struthio camelus) breeding biology in the Serengeti Ecosystem

The mean laying date was found to be significantly earlier in the western area compared to the eastern area of the Serengeti Ecosystem. The ostrich/nest ratio was not significantly different between the two areas indicating similar breeding density. Similarly the ostrich/predator ratio was also not significantly different between areas indicating that predation pressure is equally high. The ratios of predator/nest and predator/singleton were not statistically significantly different between areas suggesting that loss of nest during egg stage did not vary between areas. However, the frequencies of predators, ostriches, nests, and singletons were significantly higher compared to broods in the western area than in the eastern areas, indicating a high predation pressure in the eastern area and therefore reduced breeding success.

4.2 Paper II

The white colour of the ostrich (Struthio camelus) egg is a trade-off between predation and overheating

Ostrich, the ground nester, lay immaculate eggs which are unattended for about 2 weeks or a few more days before the onset of incubation. Temperature experiments conducted on ostrich eggs coloured differently (i.e. brown painted, white painted and others left unpainted as controls) were exposed under the sun during the day, revealed significant differences among the eggs. The egg-surface temperatures and egg core-temperatures were significantly influenced by the egg colour, time of day and the date. The surface and core temperatures of the brown eggs were significantly higher than those of the white and control eggs. The core temperature of the brown egg was as high as 45 ºC which was beyond 37.5 ºC, the temperature at which the mortality of ostrich embryos starts to increase. Indicating that brown colour would be lethal to the developing embryos. On the other hand, visibility tests conducted by the walking observer toward the eggs revealed that the mean discovery distance to the control (unpainted) egg was significantly longer than that of the brown-painted egg, indicating a higher visibility of white eggs. Since white eggs can easily be seen from long distances, predators can as well locate the eggs visually from long distances.

4.3 Paper III

Do ostriches (Struthio camelus) recognise their own eggs?

Several females lay on a nest, but only the major female together with the territorial male provide parental care from incubation to fledging chicks. In such an intra-specific brood parasitism, more eggs are laid than can possibly be incubated, and therefore some are ejected out of the nest. Movement of eggs inside the nest was found to be random, since there was no significant difference in the pattern of egg movement from inner to the outer layer and from outer layer to inner layer of the nest. Ejected eggs were generally not moved back into the nest by the major female. The ejected eggs that were experimentally put back in middle of the nests were not ejected out again. Spectrophotometric study revealed that, there was no significant difference in colour between the central inner eggs and ejected eggs. Therefore, results suggest that there is random movement of eggs in the nest and random ejection of eggs, an indication that ostriches do not recognize their own eggs.

4.4 Paper IV

Group dynamics and sex ratios in ostriches (Struthio camelus) in the Serengeti ecosystem, Tanzania

Generally the adult sex ratio (female/female+male) was found to be female skewed. Female skewed sex ratio was observed both in the national park and partially protected areas. The sex ratio in the national park, however, was significantly skewed toward females compared to the partially protected areas. There was a seasonal difference in sex ratio, where female skewed sex ratio was observed in the dry season compared to the wet season.

The most common ostrich group sizes observed composed of ≤ 4 individuals while large groups occurred occasionally. There was no significant spatial difference in group sizes. Significantly larger group sizes were observed in the wet season than in the dry season. Single males were observed more frequently during dry season compared to wet season, indicating male territorialism. However, group sizes did not vary with habitat types, i.e. between open habitat type (grassland and wooded grassland) and closed habitat type (woodland and bushland). Most ostriches occurred singly or in pairs, whereas in large groups, the majority of members of each group were females. Hence female skewed sex ratio increased with group size.

4.5 Paper V

Does illegal hunting affect density and behaviour of African grassland bird species? A case study on ostrich

Direct assessment of ostrich mortality due to illegal hunting is difficult because illegal hunters usually remove carcasses of hunted animals and scavengers rapidly consume the remains. Indirect assessment by the use of demography and behaviour has therefore been proposed as indicator of disturbance and exploitation. Analyses of the responses provided by local people through questionnaires, indicated that illegal hunting was conducted on birds (both small and large) either actively (e.g. slingshot, guns, spears) or passively (e.g. snares, birdlimes). Bird products were mainly for consumption and/or commercial purposes. With respect to ostriches, there was no significant difference in their densities between national park and partially protected areas, between wet and dry season and between open habitat (e.g. grassland, wooded grassland) and closed habitat (e.g. woodland, bushland) types. However, ostriches responded quickly and fled with longer flight initiation distance in the partially protected areas than in the national park when approached by human. This suggests that ostriches perceived humans as a threat, and therefore illegal hunting in the partially protected areas may pose fitness consequences to ostriches.

5. Discussion

5.1 Breeding biology and behaviour ecology

Results indicated that ostriches started laying significantly earlier in the low altitude western area than in the high altitude eastern area of the Serengeti National Park (Paper I), suggesting that the topography and rainfall pattern influence ostrich breeding. The rains increase towards the Lake Victoria in the western part of the ecosystem (Campbell and Hofer 1995), while the short rains may fail completely in the eastern area (Sinclair 1995). The rainfall gradient associated with the forage biomass gradient influences early breeding in the western area. The lake and the topography together generate a diversity of local climates that bring differences in rainfall distribution. Therefore, the factors which build up the female's reproductive potential and trigger her reproductive activities at the right time are predominantly the availability of sufficient food over a length of time (Sauer and Sauer 1966). Individuals need to lay eggs at the proper time so as to synchronize hatching with seasonal events and food peak (Perrins 1970; van Noordwijk et al. 1995; Drent 2006).

During the laying period, some eggs regarded as 'singletons' (i.e. eggs laid randomly outside the nests and without parental care) were found scattered in the study area. Appearance of such eggs could be attributed to prevention of minor females by major females to lay their eggs in the nests where incubation had started already or loss of nest due to predation (Bertram 1992; Sauer and Sauer 1966). However, there was no significant difference in the proportion of ostriches to predators, predators to nests and predators to singletons between western and eastern areas of the ecosystem, indicating equal predation pressure. High frequency of ostriches, predators, nests and singletons compared to broods in the eastern areas indicate a low breeding success. Though predation pressure is equal in both areas, western area has a mixture of woodland and bushy savannah that may conceal the nest and therefore reduce predation on nests. In addition, the population of large predators is lower in western compared to the eastern area (Nowell 1996, Packer et al. 2005), may as well contribute to the observed results. Therefore western area can be considered as the 'source' for ostrich production in the Serengeti ecosystem.

During the breeding period, the conspicuous white ostrich eggs are left unattended for at least two weeks from the commencement of laying. Results on the temperature experiments on ostrich painted eggs showed a significant effect of egg colour on both the surface and core temperatures during exposure to direct sunlight. Brown painted eggs had significantly higher temperatures than that of white-painted and control eggs. Egg colouration therefore suggests fitness consequences (Montevecchi 1976; Kilner 2006; Paper III) in terms of increasing embryo mortality and reduced hatching success. Although cryptic egg colouration has been explained as an adaptive anti-predator strategy in ground-nesting birds (Montevecchi 1976; Solís and de Lope 1995; Lloyd et al. 2000), the white colour of ostrich eggs seems to be adaptive to prevent overheating but prone to predation (Bertram and Burger 1981).

Ostrich communal laying system led to the nest having more eggs than could be incubated. Since ostriches can only incubate about 20 eggs (Bertram 1992; Kimwele and Graves 2003), excess eggs were ejected out of the nest at the onset of incubation. There was evidence that ostriches moved the eggs randomly inside the nest and ejection of the eggs from the nest was random. There was no spectral reflectance difference in birds' visible range between ejected and inner central eggs, an indication that ostrich eggs are similar in colour and therefore colour can not be used as a cue to reject minor female's eggs. Therefore the hypothesis that major female ostriches recognise their own eggs and eject others by differentiating egg colours was not supported by the study. However, in order for ostrich to reduce probability of making errors by ejecting its own eggs, acceptance of foreign eggs can be optimal as long as the number of eggs is below a certain threshold level (Bertram 1979; 1992; Davies et al. 1996).

5.2 Sex ratio and group dynamics

The observed female biased sex ratio for ostriches in the Serengeti Ecosystem supports previous studies (Hurxthal 1979; Sauer and Sauer 1966; Bertram 1992). Though both areas showed a female skewed sex ratio, the national park was highly skewed compared to the partially protected area (Paper IV). Skewed sex ratio indicates differential mortality between sexes, and that males are prone to predation due to their behavioural trait (Bertram 1992). Highly skewed sex ratio in the national park could be attributed by high density of large predators (Nowell and Jackson 1996; Nyahongo 2004; Packer et al. 2005). Territorial behaviour of males and their conspicuousness expose them to high predation risk (Bertram 1992). The female biased sex ratio in the dry season can as well be explained by male predation. Dry season coincides with breeding season, when males become solitary and occupy territories thereby increasing predation risk (Bertram 1992). This has been supported by the results where there was higher frequency of single males during dry than wet season.

Paper (IV) further describes variation of ostrich group size with respect to area. Non significant difference in group sizes between the national park and the partially protected areas, indicate that ostriches do not respond by forming larger groups in the partially protected areas despite increased hunting pressure. However, several other factors may influence group sizes, for example, mating system and availability of forage are among the variables, where areas rich in food supply are associated with larger group sizes compared to poor ones (Gude et al. 2006). Increased group size has been suggested to confer many benefits, but group members may also incur various costs, especially through competition for resources with other group members (Krause and Ruxton 2002). Benefits from group membership could be in the form of reduced predation risk via increased vigilance or dilution effects (e.g. Hamilton 1971; Pulliam 1973; Kenward 1978; Bertram 1980; Caro 2005).

Larger groups were observed in the wet season than in the dry season which is in accordance with previous studies (Nagy and Knight 1994; Bergström and Skarpe 1999). Spatial and temporal distribution of quantity and quality food supply (Fryxell and Sinclair 1988) can be regarded as driving factors of group sizes, in addition to increase in natal recruitments.

5.3 Effect of illegal hunting on ostrich density and behaviour

Although the densities of ostriches were not significantly different between national park and partially protected area, results indicate that in the partially protected areas, ostriches were more wary and had longer flight initiation distance than in the national park (Paper V). Partially protected areas have been heavily impacted by illegal hunting (Caro 1999b; Holmern et al. 2007), and that hunting has been mainly for subsistence and/or commercial purposes (Loibooki et al. 2002). High hunting pressure increases disturbance levels that might have indirect effects on animal survival. Disturbances divert time and energy from foraging, parental care and mating displays (Steidl and Anthony 2000), increase stress hormone levels (Buchanan 2000) and therefore reduce survival and reproductive success (Lima and Dill 1990; Morris and Davidson 2000). In some areas disturbances might cause animals to shift to more protected areas, which may be lower in quality or have a higher risk of predation (Sinclair and Arcese 1995). Similar findings where animals are more flighty in exploited areas have been reported in other studies (Caro 1999a; de Boer et al. 2004; Donadio and Buskirk 2006; Setsaas et al. 2007).

6. Implications for management and conservation

The current study has shown that the majority of ostrich broods are seen within the western area of the Serengeti ecosystem. This implies that there is a higher survival of ostrich nests in western compared to other parts of the ecosystem. The vegetation type (plain short grasslands) together with high population of large predators in eastern part of Serengeti probably contributes to the great loss of nests. Due to the fact that the ostrich do take long distance movement, they might be migrating to other parts and mix with other ostriches in the ecosystem. The management authority needs to protect western area that acts as a ‘source’, as well as maintaining the interconnectedness between the areas to allow free movements of birds and other animals, since maintaining adequate habitats for such diverse group of species, other groups of wildlife would also benefit.

Adult sex ratios provides a potential tool for monitoring habitat suitability. Fragmentation has been found to influence adult sex ratio of other birds (Zanette 2001) and mammals (Banks et al. 2005). Habitat degradation leads to increased exposure of nests to predators and competitors resulting into higher mortality and consequently a skewed adult sex ratio. More information is needed on the frequency of sex ratio skew on the stability of adult sex ratio in space and time, and finding means of estimating adult sex ratio in an unbiased way.

The behaviour of birds towards humans mirrors the behaviour of humans towards birds. If humans disturb birds through hunting for example, they will respond by fleeing at the sight of them (Frid and Dill 2002; Ikuta and Blumstein 2003). It was found that, ostriches were flighty in partially protected areas where illegal hunting is practiced. Results through questionnaires on illegal hunting revealed that illegal hunters access partially protected areas and the national park to hunt birds including ostriches. The fact that the ostriches in the partially protected areas fled immediately after visually detecting the human being confirmed that they perceived humans a threat.

Flight response displayed by ostriches can be a useful indicator of the status of other herbivores such as buffalos (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), zebras (*Equus burchelli*), grant gazelles (*Gazella granti*), hartebeest (*Alcelaphus buselaphus*), Thomson’s gazelles (*Gazella thomsoni*) and warthogs (*Phacochoerus africanus*) which are constantly found in association with ostriches. However, effectiveness of this indicator depends on hunting pressure and hunters’ preferences for certain species (Ndibalema and Songorwa 2007). Flight behaviour can therefore be used to monitor the success of conservation measures, since monitoring the frequency of flight behaviour is an inexpensive method and easy to apply.

7. Future prospects

Detailed evidence for the effect of climate change on birds comes from studies of the timing of breeding (Dunn 2004). Climate change has led to shifts in phenology in many species across taxonomic groups (Visser and Both 2005). However, the magnitude of the response among species and locations remains inadequately known. Therefore, there is a need to establish extensive studies to monitor the effects of climate change in relation to food availability over large areas and determine how climate change affects the reproductive performance of species throughout their ranges.

Long term studies are recommended to examine the existence of the ostrich metapopulations (groups of spatially separated population of the same species that interact at some level) in the Serengeti ecosystem. In addition, much more remains to be discovered with respect to ostrich adult sex ratios in relation to persistence of the population.

There is ample scope for many interesting detailed investigations on the ostrich population regarding chick survival and adult male movements. Future studies should consider use of radio transmitters (GPS radio collars) in chicks and adult males to monitor their survival and movements respectively. By monitoring the movement of males it will be easier to obtain nests because territorial males would always go back to the nests. Tracking males will also lead to the investigation whether they are resident or migratory between breeding seasons.

Human disturbance such as illegal hunting can affect avian abundance and reproductive success through for example, avoidance of potential feeding patches, decreased amount of foraging time and decreased parental care to the chicks. Flight initiation distance is an excellent and easy-to-measure metric that quantify an individual's fearfulness in a particular situation. Wildlife managers therefore need to use flight initiation distance to identify set back zones – areas beyond which species are not disturbed by human. However other key aspects such as alert distance and scanning rate may be used in measuring individual behaviours.

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PAPER I

Breeding biology of ostriches (*Struthio camelus*) in the Serengeti ecosystem

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Abstract Details regarding ostrich (*Struthio camelus*) breeding biology is poorly known. We studied ostrich breeding behaviour in Serengeti, Tanzania to investigate possible differences in laying dates between low altitude and high altitude populations. Ostriches in western area (WA) laid eggs significantly earlier than those in the eastern area (EA). The differences could be attributed to topography and rainfall pattern. Reliable rains in lower altitudes influenced by Lake Victoria ensure availability of food that in turn influences the whole process of the reproductive cycle. Clutches were contributed by several females with a nest having up to 38 eggs. The average combined clutch size was 27 and 26 per nest in WA and EA respectively. We also compared the frequency of observation of predators, ostriches, nests, 'singletons' (single eggs laid randomly outside the nest) and broods between the two areas. There was no statistically significant difference between WA and EA in 1) the ostrich/nest ratio, indicating similar breeding densities; 2) ostrich/predator and predator/nest ratios, indicating that predation pressure was equally high; 3) nest/singleton and predator/singleton ratios, indicating that loss of nests during egg stage did not vary between areas. However, there were significantly more predators, nests and ostriches compared to broods in EA than in WA, indicating a significantly lower reproductive success in EA. Using metapopulation terminology, ostriches in EA should be regarded as a 'sink' population and those in WA as a 'source' population. Thus, we propose limiting future development in the WA.

Keywords: breeding, ostrich, predation, Serengeti, *Struthio camelus*

Introduction

Ostriches *(Struthio camelus)* practise communal breeding, which involves several females laying in the same nest (Bertram, 1992; Kimwele & Graves, 2003). The territorial male prepares several scrapes on the ground out of which one becomes a nest where the female lay her eggs (Bertram, 1992). The first female to lay in the nest is referred to as the 'major' female while females that subsequently lay in the same nest are regarded as 'minor females'. However, only major females and territorial males provide parental care (Sauer & Sauer, 1966; Bertram, 1992). Ostriches generally breed during the dry season between July and October (Brown & Britton, 1980). The major female ostrich on average lays 11 eggs (range 8-16) (Bertram, 1992), while one to seven minor females may lay 20-40 additional eggs in the nest considerably in excess of the number that can be incubated (Sauer & Sauer, 1966; Hurxthal, 1979; Bertram, 1992). The clutch size in ostrich nests before incubation is indeterminate, but a nest may contain up to 30-40 eggs (Leuthold, 1977; Bertram, 1979). Other ratites also have communal nesting systems with multiple females laying in one nest, but only the male undertake incubation and parental care responsibilities (Coddington & Cockburn, 1995).

Through evolution, the timing of avian breeding seasons has generally been adjusted to maximize the number of young produced (Perrins 1970). Breeding is a demanding process both in terms of energy and nutrient requirements particularly during egg formation (Nager, 2006). Breeding individuals should adjust their behaviour to maximize their expected lifetime reproductive success (Williams, 1966). It is well known that food availability is a supplemental factor which can influence the timing of egg laying in birds (Perrins, 1970; Boutin, 1990; Svensson, 1995). Perrins (1970) argued that most individuals were initiating their breeding season too late for the offspring to profit fully from the seasonal peak of food abundance, and suggested that the proximate cause was a shortage of food for females when forming eggs (the food constraint hypothesis). However, increasing spring temperatures over the past decades confirm responses in many but not all migrant bird species, and where detailed data are available the advance documented in laying date seems often to fall short of the shift in the food peak (Drent, 2006). Some migrant species are unable to track the advancing phenology of the vegetation (and presumably prey abundance) (Visser *et al.*, 1998; Sanz *et al.*, 2003; Visser & Both, 2005). However, other investigations have revealed significant advances in egg laying date in some species (Slater, 1999; Both & Visser, 2001).

Perrins (1970) suggested that "the date at which each individual actually lays is related to the food supply at the time of laying since laying can not begin until food has become sufficiently abundant for each female to find enough food". Areas in the north-western part of Serengeti National Park (SNP) receive a lot more rains due to the influence of the topography and proximity to Lake Victoria than the south-eastern part of the ecosystem (Campbell & Hofer, 1995). Early rains and therefore early availability of food in the north-western part should trigger earlier breeding here than in areas of the SNP that receive less rains, which is particularly relevant for the eastern area. However, laying date must be viewed as a trade-off between opposing seasonal trends affecting both parents and their offspring, i.e. a trade-off in the fitness payoffs for offspring against those of the parents (Partridge, 1989). Abundant nourishment is needed, not only for nestlings and juveniles, but also to meet increased energy demands of breeding adults (Ehrlich *et al*., 1988). For females, those increased demands include the energetic burden of producing eggs (Nager, 2006; Perrins, 1996), whereas males need additional energy to support vigorous displays to defend territories and for displays related to sexual activities (Andersson, 1994; Cotton *et al*., 2004; McGlothlin *et al*., 2007). In case parental decisions are based on the costs and benefits of parental care, avian nest desertion should occur when the cost of attending the nest results in a reduction of parental fitness (Clutton-Brock, 1991). In avian species, most desertions occur during the clutch stage (Ricklefs, 1977). Factors that cause clutch desertion include lack of food (Anderson, 1989), low quality of parents (Wiggins *et al*., 1994) and partial clutch loss (ten Cate & Taborsky, 1992; Fernández & Reboreda, 2000).

Although ostrich nests are well camouflaged and surprisingly hard to detect, they generally experience high predation (Bertram, 1992). Spotted hyenas (*Crocuta crocuta*), Egyptian vultures (*Neophron percnopterus*) and lions (*Panthera leo*) are the main predators of ostrich eggs (Bertram, 1992). Nests are located visually or other cues may be used such as observing parental activity like building and leaving or returning to nests with eggs or young (Collias & Collias, 1984; Martin *et al*., 2000). Most large top predators are confined to protected areas, or to regions remote from human activity (Nowell & Jackson, 1996; Nyahongo, 2004). In areas with high densities of predators, frequency of ostrich nest predation may be high. Although, it is not known if the increased nest predation may lead to increased number of 'singletons' due to disturbance created to the female in urge to lay. 'Singletons' are hereby referred to as single eggs laid randomly outside the nest. It could be expected that more singletons are laid in areas where nest predation is high, and therefore predation can be regarded as one of the main factors that can influence reproductive success within various populations (see also Sauer & Sauer, 1966).

The most comprehensive studies on ostriches include physiology, anatomy, ostrich farming and pathology (Siegfried & Frost, 1974; Bezuidenhout 1986; Brown *et al.*, 1993; Degen *et al.*, 1994; Deeming 1995), while little attention has been directed to ostrich breeding biology in the wild (but see Sauer & Sauer 1966; Leuthold, 1977; Jarvis *et al.*, 1985; Bertram 1992). Here, we investigated possible differences in Masai ostrich (*S. c. massaicus*) breeding biology in low and high altitude areas in SNP, Tanzania. In more detail, we examined possible differences in egg laying date between low altitude and high altitude areas. In addition, we compared the frequency of predators, ostriches, nests, singletons and broods between the two areas. Finally, we estimate the reproductive success of ostriches by monitoring all nests found until we could determine the fate of the nests.

Methods

Study area

The study was carried out in the Serengeti National Park (SNP) (14,763 km^2) and adjacent Ikorongo (563 km^2) and Grumeti (416 km^2) Game Reserves and Ikoma Open Area (600 km^2) from May 2005 to December 2006. However, the study area was divided into two areas; low altitude western area (WA) and high altitude eastern area (EA) (Fig. 1). In both areas, the climate is usually warm and dry with mean temperatures varying between 15°C to 25°C. The rains in the Serengeti ecosystem falls in a bimodal pattern, the short rainy season between November and January, and the long rainy season between March and May when there is heavy downpour (Norton-Griffiths *et al.*, 1975). However, the rains increase towards Lake Victoria and can fuse into one long period, particularly in the northwest, or the short rains can fail entirely especially in the southeast (Sinclair, 1995). There is an overall rainfall gradient from the dry south-eastern plains (800 mm per year) to the wet north-western area (1,050 mm per year) of the SNP (Campbell & Hofer, 1995). During the study period, EA received an average rainfall of 744.6 mm whereas WA received an average rainfall of 882.5 mm per year (Data from Tanzania National Park Authority meteorological stations). The mean altitude in the WA is 1,205 m and in the EA 1,653 m above sea level (Sinclair, 1995). The WA is characterised by wooded grasslands and woodlands dominated by *Acacia* species whereas EA is dominated by plain grasslands (Herlocker, 1976).

Field sampling

While driving around in the study area, we systematically recorded all sighted ostriches, nests, broods, singletons and predators (i.e. lions and hyenas, whereas Egyptian vultures were not observed in the study area). Nests, singletons and broods were accurate data in which each observation was one nest, singleton, and brood respectively. Lions, hyenas and ostriches are sometimes observed in dense vegetation hence some individuals of a herd/group may have been overlooked. Therefore we equalled each observation, regardless of number of individuals, to one for use in the analyses.

During each breeding season (i.e. from July to October which sometimes extended to December) we searched intensively for nests throughout the study area. Nests were defined as scraped shallow pits with egg(s), whereas singletons were eggs that were randomly laid directly on the ground without any indication of scrapes in the vicinity. Different methods were used to find nests (Table 1), however, all singletons were encountered by chance. Once a nest or singleton was discovered, GPS position was taken to allow subsequent visits. Visits were kept brief and as infrequent as possible in order to minimize the risk of investigators inducing nest desertion. We visited nests and singletons once a week, so as to minimize disturbance for the laying and incubating birds. Each time we visited the nests we recorded the total number of eggs.

We indirectly estimated the laying date based on number of eggs in the nest. The assumption was that the first three eggs were laid by the major female, each egg after every second day, before the minor females started laying (Bertram, 1992). From the total number of eggs in the nest we calculated the probable laying date by backdating considering the first five days that the major female laid her first three eggs.

Data analyses

We used Kolmogorov-Smirnov tests to investigate if our data deviated from normality. The laying dates were found to be normally distributed, and therefore we used Student t tests for comparison of laying dates between the two areas. Because of small sample size in WA we used Mann Whitney U tests for comparison of clutch size between the areas at the onset of incubation. Pearson Chi-square tests were used to compare the frequency of predators and that of the ostriches, nests, singletons, and broods between WA and EA. Between year comparisons were not possible due to low sample sizes. However, there is no reason that number of individuals of these sedentary animals should change much between two years only, and therefore we pooled the data for further analyses. For analysis of laying dates we only considered 2006 nests because of adequate sample size in this year only. SPSS 14 was used for statistical analyses. All values are presented as mean ± standard deviation ($\overline{X}$ ±SD), and all analyses are two-tailed.

Results

Laying date and clutch size

During the study period we obtained a total of 57 nests and 37 singletons. In 2005 there was a total of 33 nests (30 in EA and 3 in WA) and 21 singletons (20 in EA and 1 in WA), whereas in 2006 there was a total of 24 nests (14 in EA and 10 in WA) and 16 singletons (10 in EA and 6 in WA) (Fig. 1). Mean ostrich laying date in 2006, was significantly earlier in WA (August 28 ± 21 days, N = 10) than in EA (September 17 ± 24 days, N = 12) (t = -2.05, df = 20, P = 0.05), although this was not tested for the year 2005 due to lack of independence in the data (small sample size particularly in the WA). When considering the whole study area, the average clutch size was 25.9 ± 4.8 eggs (range = 20-38, N = 18) in the nests where laying had ended and incubation started. In WA the clutch size was 26.8 ± 3.0 eggs (range = 23-30, N = 4) whereas in EA it was 25.6 ± 5.2 eggs (range = 20-38, N = 14). The average clutch size in the two areas was not statistically significantly different (Mann Whitney U = 19.5, Z = -0.91, P = 0.37).

Relationship between frequency of observations of predators, ostriches, nests, singletons and broods

There were 40.0 ostrich observations (N = 1765) per nest (N = 44) in EA, compared to 55.4 ostrich observations (N = 720) per nest (N = 13) in WA. However, the difference was not statistically significant (χ^2 = 1.03, df = 1, P = 0.31), indicating comparable breeding densities in the two areas.

There were 12.0 ostrich observations (N = 1765) per predator (N = 147) in EA, compared to 12.6 ostriches (N = 720) per predator (N = 57) in WA. This difference was not statistically significant (χ^2 = 0.10, df = 1, P = 0.75). Furthermore, there were 3.3 predators (N = 147) per nest (N = 44) in EA, compared to 4.4 predators (N = 57) per nest (N = 13) in WA. Again, this difference was not statistically significant (χ^2 = 0.60, df = 1, P = 0.44). These results suggest that the predation pressure was equally high in the two areas.

There were 1.5 nests (N = 44) per singleton (N = 30) in EA, compared to 1.9 nests (N = 13) per singleton (N = 7) in WA, a difference that was not statistically significant (χ^2 = 0.2, df = 1, P = 0.65). Furthermore, there were 4.9 predators (N = 147) per singleton (N = 30) in EA, compared to 8.1 predators (N = 57) per singleton (N = 7) in WA. Again, this difference was not statistically significant (χ^2 = 1.31, df = 1, P = 0.25). These results indicate that loss of nests during egg stage did not vary between EA and WA.

There were 36.8 predators (N = 147) per brood (N = 4) in EA, compared to 5.2 predators (N = 47) per brood (N = 9) in WA, a difference that was statistically significant (χ^2 = 12.50, df = 1, P < 0.001). Furthermore, there were 11.0 nests (N = 44) per brood (N = 4) in EA, compared to 1.4 nests (N = 13) per brood (N = 9) in WA. The difference between areas was statistically significant (χ^2 = 10.59, df = 1, P = 0.001). Finally, there were 441.4 ostriches (N = 1765) per brood (N = 4) in EA, compared to 80.0 ostriches (N = 720) per brood (N = 9) in WA and the difference between areas was statistically significant (χ^2 = 10.14, df = 1, P = 0.001). All these results indicate a significantly lower reproductive success among ostriches in EA than in WA.

Fate of the nests

None of the observed nests in any of the areas reached hatching stage, and predation accounted for more than 80 % of nest destruction (total N = 47). In the WA 11 out of 13 nests (84.6 %) were predated, while in EA the corresponding number was 36 out of 44 nests (81.8 %) (Fig. 2). The remaining nests were either abandoned (WA: 1 nest (7.7 %); EA: 8 nests (18.2 %) and only one nest (7.7 %) in WA had unknown fate since we left it intact after completion of the field work. All singletons where abandoned unless predated (Fig. 2). Some of the nests were partially predated and thereafter abandoned, whereas other nests were just abandoned.

Discussion

Generally ostriches breed during the dry season. In East Africa, and Serengeti in particular, ostriches mainly lay between July and October (Bertram, 1978; Brown & Britton, 1980; Bertram, 1992). However, we also found nests being initiated until December. Sauer and Sauer (1966) found that in the arid areas of Namibia, the overall peak in reproductive activity was just before the main rainy season of August to November. Smit (1963) recorded that the domesticated birds in the South African Little Karroo region mainly were laying from June or July until September, but some eggs appeared in nearly all months. Hurxthal (1979) recorded *massaicus* ostriches breeding mainly from September to December with a peak in early November. The laying period reported by Jarvis et al. (1985) for South African ostrich in Zimbabwe was mainly from July to December or early January.

Our results indicate that ostriches started laying significantly earlier in the WA than in the EA suggesting that the altitude and rainfall gradient associated with the gradient of the grassland growing season, have an influence on ostrich breeding in the ecosystem. The grassland growing season, as measured by the occurrence of live forage biomass increases towards the northwestern area (McNaughton, 1985; McNaughton & Banyikwa, 1995). When food supplies have been lastingly rich in the area, the main ostrich reproductive period builds up gradually, and all this occur towards the end of the dry season and long before the first rains fall (Sauer & Sauer, 1966). Since there is a strong selection pressure to lay eggs at the proper time (Dunn, 2004; Visser & Both, 2005; Drent, 2006), individuals need to synchronize hatching with seasonal events such that the period of maximal demand of the young coincides with the food peak (van Noordwijk et al., 1995). Ostriches are opportunistic breeders, laying soon after a localized flush of green following rains (Sauer & Sauer, 1966). This greener vegetation reappears earlier in the western area than in the eastern area due to presence of short rains (that may fail in the eastern area) in the late dry season. Most individual females in areas richer in food than others, will tend to breed earlier than others in successive seasons each year (Perrins, 1970). The factors which build up the female's reproductive potential and trigger her reproductive activities at the right time are predominantly the availability of sufficient food over a length of time (Sauer & Sauer, 1966). However, birds must not only collect specific nutrients for egg formation, but must do so over a brief period when food may not yet be plentiful (Perrins, 1970; 1996).

In the present study, the average clutch size ranged from 20-38 (18 nests), which is more or less similar to the clutch size reported by Bertram (1978) for *massaicus* ostrich in Tsavo National Park that varied between 20 and 36 eggs. Hurxthal (1979) rerecorded average clutch sizes for *massaicus* in two years as 35.5 (13 nests) and 47.0 (14 nests). However, there were cases where a number of singletons were laid outside the nests. Occurrence of these singletons might have been attributed to major female reluctance to allow minor females to lay additional eggs after the incubation start or nest predation. We did not witness a major female denying a minor female from laying on her nest, although Bertram (1992) observed major females being reluctant to leave their nests after the incubation start, whereas Sauer and Sauer (1966) emphasized that singletons could be a result of exhaustive runs from sources of danger or by hens lacking a mate. However, the ratio of predators to singletons and predators to nests did not differ significantly between the two areas suggesting that loss of nests due to predators that might have led to the occurrence of singletons did not vary between the areas.

Nest predation was extremely high in the SNP; ~ 80 % of the nests were predated. Female ostriches never laid in a previously predated nest, and therefore it is reasonable to conclude that a female on the urge to lay an egg but finds her nest predated or partially predated will lay a singleton egg outside the nest or potentially into the nest of another major female. These singletons were commonly found randomly scattered not even close to the already established nests. This situation is different from one where eggs are ejected and scattered outside the nests some few meters away at the onset of incubation when excessive eggs are laid communally than can be incubated (see also Sauer & Sauer, 1966; Bertram, 1992; Kimwele & Graves, 2003). In addition, all singletons together with some nests were abandoned, probably due to the partial predation of nests in particular, or spread of eggs by golden jackals (*Canis aureus*) or black backed jackals (*C. mesomelas*) which mainly played around with eggs but could not crush them (F. Magige et al., pers. comm.). However, we have no evidence that nests desertions were due to our frequent visitations. In common with ostriches, rheas also have high rates of nest desertion during the laying stage (Fernández & Reboreda, 2000). Studies on rheas have shown a high rate of nest desertion commonly associated with egg predation particularly in the early laying stages (Fernández & Reboreda, 2000; Fernández & Reboreda, 2002; Sales, 2006). The difference between rheas and ostriches is that most cases of nest desertion in rheas were associated with the loss of a few eggs and therefore the male had the possibility of continuing incubation (Fernández & Reboreda, 2000) whereas in ostriches nest desertion was the result of nest destruction (desertion was compulsory).

There was no significant difference between the ratio of ostriches to nests between WA and EA, indicating similar breeding densities. However, fewer nests were obtained in the WA, which might be attributed to the difficulty of discovering nests in the densely vegetated western corridor, suggesting that visibility of eggs was a major factor in their discovery. Therefore, nest density in WA could potentially be significantly higher than the one observed. The ratio of ostriches, predators, nests and singletons to broods were significantly different between the two areas with high frequency of broods in the western area indicating that the reproductive success was quite high in the western area. The results obtained in this study indicate an existence of metapopulation dynamics in the Serengeti ecosystem, where the western area can be regarded as a 'source' and eastern area as a 'sink' population. Source-sink dynamics are used to describe how variation in habitat quality, competitors or predators may affect the population growth or decline of organisms in space (Dias, 1996; Hanski, 1999). Therefore predation is one of the main factors that can influence reproductive success within various populations.

Conclusion

Food supply for females is one of the proximate drivers of laying date. Availability of adequate food supply triggers advanced laying date for ostriches, the case observed in the western area. However, climate change has led to shifts in phenology in many species across taxonomic groups (Visser & Both, 2005). Much of the evidence for effects of climate change on birds comes from studies of the timing of breeding. Since many species of birds tend to have advanced laying date in years with warmer temperatures (Dunn, 2004; Drent, 2006), studies are needed on climate change coordinated to food availability and breeding ecology in monitoring the relationship between change in timing of breeding and population dynamics of ostriches. In addition, the proportionally large number of broods observed in the western area suggests high hatching success and low predation rate on nests and chicks in this area. Therefore, topography, rainfall and predation seem to influence the ostrich population in the Serengeti, and our results point out that the western area is likely to be a 'source' population. It is hereby recommended that care should be taken by wildlife managers to preserve the western area and maintenance of the western corridor connectivity to perpetuate free migration of birds and other animals into less productive areas.

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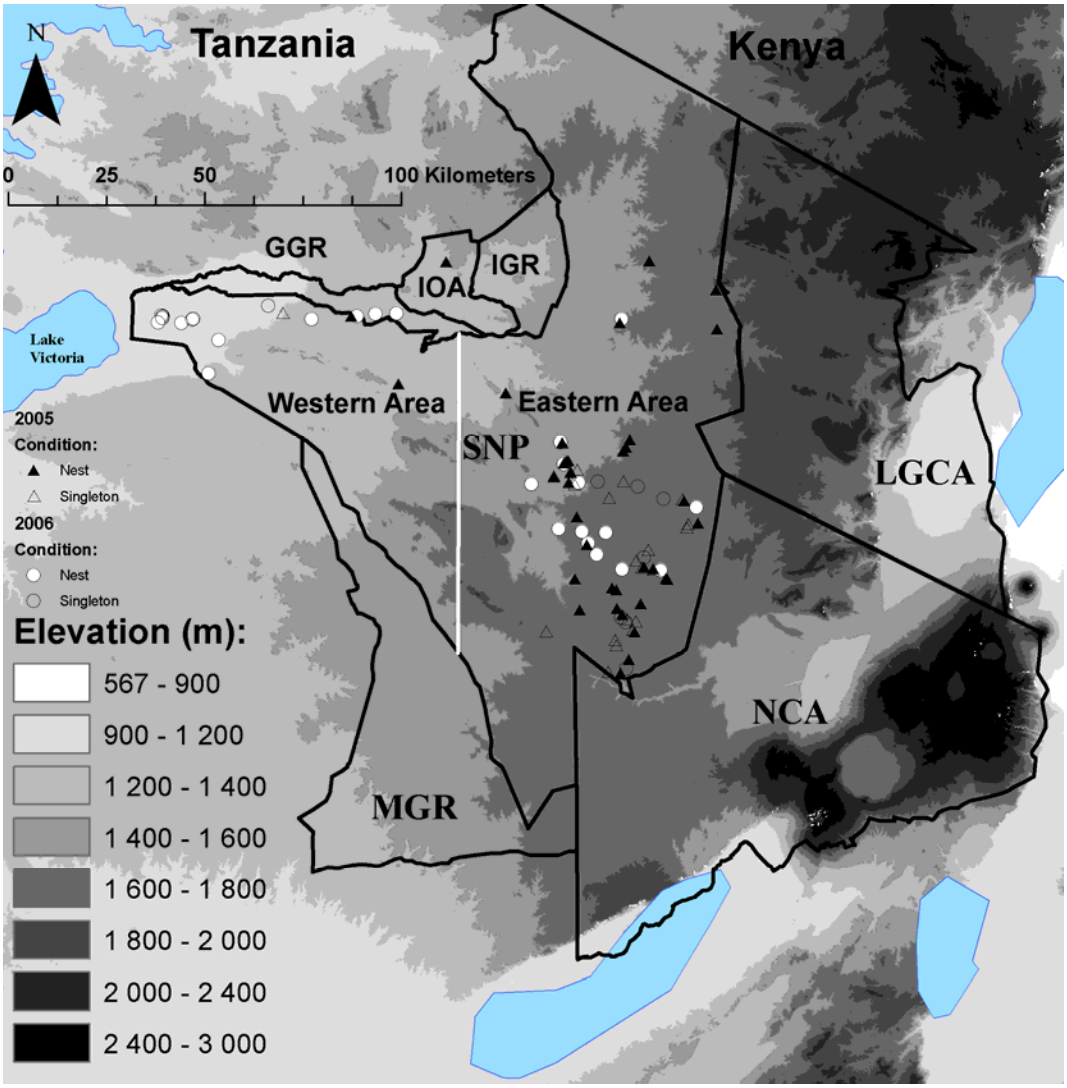
Table 1. Methods used to find nests in eastern and western areas of the Serengeti ecosystem in 2005 and 2006. Figures are percentages with number of observations in parentheses.

Method	Western area		Eastern area	
	2005	2006	2005	2006
Head of incubating ostrich observed while driving by	33.3 (1)	0 (0)	3.3 (1)	14.3 (2)
Watching a male and female sitting and standing at a particular point repeatedly	33.3 (1)	30 (3)	46.6 (14)	28.5 (4)
Chance encounter of nest when driving by	0 (0)	40 (4)	16.7 (5)	21.4 (3)
Aerial searching with plane	0 (0)	0 (0)	0 (0)	7.1 (1)
Told by Tanzania National Parks (TANAPA) rangers or other researchers	33.3 (1)	30 (3)	33.3 (10)	28.6 (4)
Total	100 (3)	100 (10)	100 (30)	100 (14)

Figure legends:

Fig 1. Map showing the Serengeti National Park and adjacent Ikorongo and Grumeti Game Reserves and Ikoma Open Area (thick black line). The white line separates the areas with low altitudes to the west and those with high altitudes to the east. Symbols denote the location of nests in both 2005 and 2006.

Fig. 2. Fate of nests and singletons during the ostrich breeding season in the western and eastern areas of the Serengeti National Park.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Tanzania
Kenya
0
25
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GGR
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Western Area
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2005
Condition:
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Singleton
2006
Condition:
Nest
Singleton
Elevation (m):
567 - 900
900 - 1 200
1 200 - 1 400
1 400 - 1 600
1 600 - 1 800
1 800 - 2 000
2 000 - 2 400
2 400 - 3 000

Fig. 1

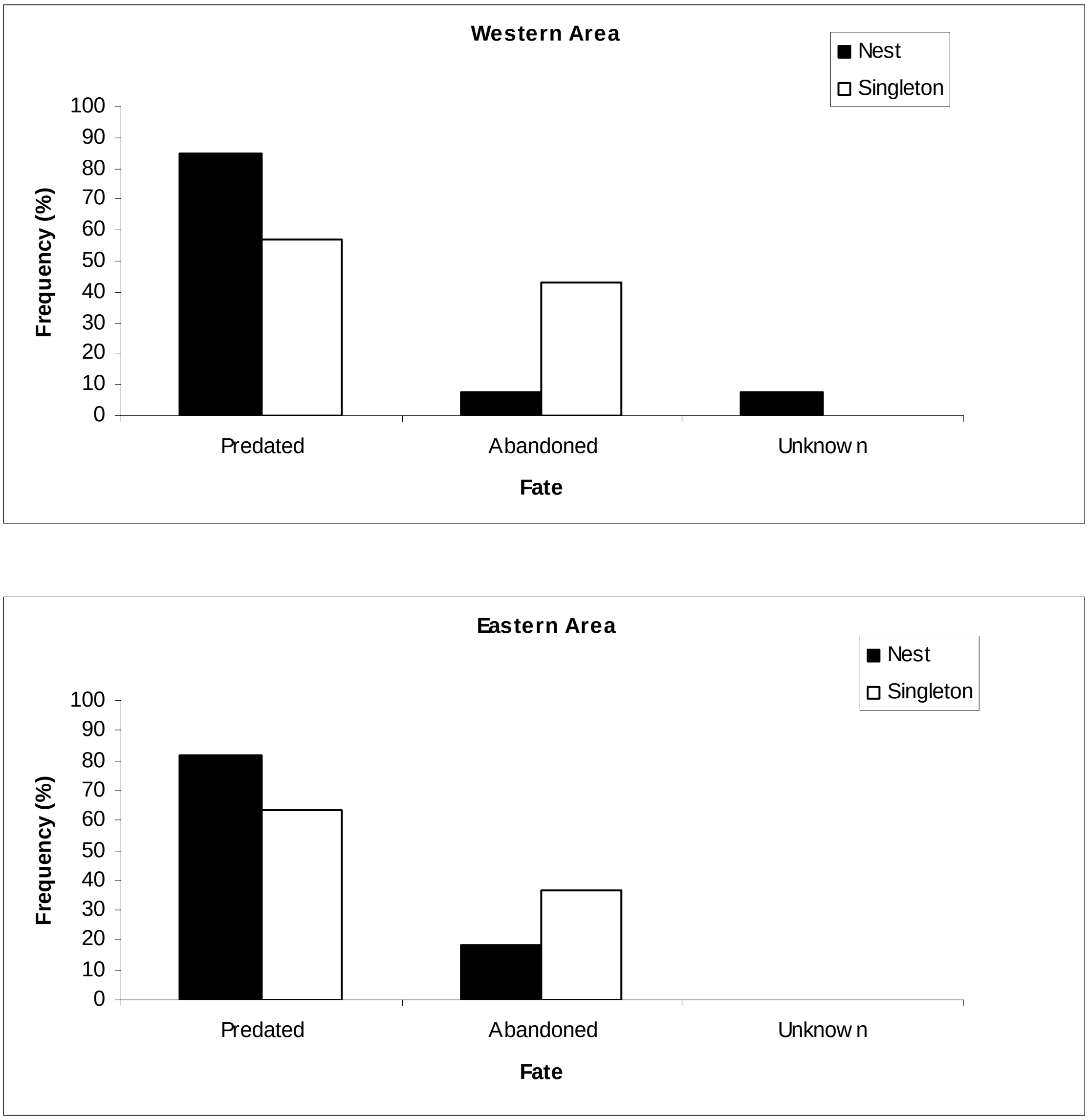
Western Area
■ Nest
☐ Singleton
Frequency (%)
100
90
80
70
60
50
40
30
20
10
0
Predated
Abandoned
Unknow n
Fate
Eastern Area
■ Nest
☐ Singleton
Frequency (%)
100
90
80
70
60
50
40
30
20
10
0
Predated
Abandoned
Unknow n
Fate

Fig. 2

PAPER II

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ORIGINAL ARTICLE

The white colour of the Ostrich (*Struthio camelus*) egg is a trade-off between predation and overheating

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Abstract Most ground nesters lay pigmented eggs, and egg pigmentation generally matches the environment. Pigmentation of eggs has evolved as a protective device against predation, but dark-pigmented eggs can be susceptible to overheating when exposed to solar radiation. The Ostrich (*Struthio camelus*) lays white eggs that are unattended for the first few weeks before incubation, and are quite visible to predators. To evaluate the effect of colour on the surface and core temperatures, we painted some Ostrich eggs dark brown or white, and left some unpainted (control), and exposed all of them directly to the sun during the day. The surface and core temperatures of brown eggs were significantly higher than those of the white-painted and control eggs. In addition, the core temperature of brown eggs exceeded 37.5°C, which is the temperature at which embryo mortality starts to increase. In a second experiment, we placed eggs (brown-painted and control) in various types of vegetation to study their visibility to an observer walking towards them. The white eggs were discovered from a significantly longer distance than the brown eggs, indicating that the predation risk may be much higher for white eggs. The results thus suggest that white eggs minimise overheating and allow the Ostrich to leave its eggs unattended before incubation starts, but they are more susceptible to predation.

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Keywords Eggs · Ostrich · Predation · Serengeti · Temperature

Introduction

Most ground nesters have pigmented eggs, whereas species nesting in deep holes generally lack pigmentation and markings (Lack 1968; Kilner 2006). Pigmentation of eggs has evolved as a defence against brood parasitism (Rothstein 1990; Davies 2000), as a structural component of shell strength (Gosler et al. 2005), as protection against potentially harmful solar radiation (Gosler et al. 2005; Kilner 2006) or as an anti-predator strategy (Portmann 1959; Caro 2005; Kilner 2006). Ground nesters suffer more predation than birds nesting off the ground (Martin 1993). Egg crypsis is therefore a probable explanation in the case of ground-nesting birds, because the colour of the eggshell provides concealment and minimises nest predation (Bertram and Burger 1981; Götmark 1992, 1993; Lloyd et al. 2000).

Although egg pigmentation reduces predation risk, a dark surface generally absorbs more radiant heat than a white one. Since the ground-nesting Ostrich (*Struthio camelus*) lays white eggs on nests that are generally exposed on grass plains for almost 2 weeks before incubation starts (Bertram 1992; own observations), the eggs are exposed to intense solar radiation. The survival of unattended avian eggs depends on their thermal properties and on how resistant the embryos are to extreme temperatures. Avian embryos can be very tolerant to hypothermia, but are far less tolerant to hyperthermia (Webb 1987). The optimum temperature for Ostrich egg incubation is 36.0–36.5°C (e.g. Deeming 1993; Hassan et al. 2004), and incubation temperatures above 37.5°C increase the incidence of dead embryos (Hassan et al. 2004).

The white colour of the Ostrich egg is thought to reduce the risk of it overheating during the period when the eggs are unattended, but it is also believed to make it more visible to predators (Bertram and Burger 1981). Spotted hyenas (*Crocuta crocuta*), Egyptian Vultures (*Neophron percnopterus*) and lions (*Panthera leo*) are the main predators of Ostrich eggs (Bertram 1992), and visually locate nests by directly spotting unattended eggs and/or observing parental activity (Collias and Collias 1984; Martin et al. 2000).

In this study, we conducted experiments on the egg temperature and predation risk to test the hypothesis proposed by Bertram and Burger (1981) that the white colour of Ostrich eggs is a trade-off between overheating and predation risk. The egg temperature experiment followed the approach used by Bertram and Burger (1981), but differed in the temperature equipment, the site (Serengeti National Park vs Oudtshoorn, South Africa and Tsavo West National Park, Kenya), the experimental eggs (dark-brown painted, white-painted and unpainted control eggs vs medium-brown painted and unpainted control eggs), the sample size (6 vs 2 eggs), the number of days with egg-core temperature measurements (4 days vs 1 day), the statistical approach (mixed linear model vs descriptive statistics) and the predation experiment (visibility test vs natural predation).

We measured the surface and core temperatures of brown-painted, white-painted and control (natural colour) eggs on different days and at different times of the day to test whether brown eggs were more likely to overheat. Our predation experiment was conducted as a visibility test where we determined at what distance brown-painted and control eggs were discovered by a walking observer. We assumed that if the human observer discovered one egg colour from further away than the other, the predators would also discover this egg colour more easily.

Methods

Study area

The experiments were conducted in the Ikorongo (563 km^2) and Grumeti (416 km^2) Game Reserves, northwest of the Serengeti National Park, northern Tanzania, during the period 5–12 December 2006. Six eggs of almost identical volume (mean 1,299 cm^3, SE ± 14) were collected from different abandoned nests in the game reserves. We only collected six eggs because of the strict regulations in the protected areas, and for conservation purposes. Two of the eggs were painted dark brown and two white (oil-based Gold Star paint; Gold Star, Dar es Salaam, Tanzania), and the remaining two were left without paint as controls. The temperatures of the egg surface, the egg core and the ground surface were measured with copper–constantan thermocouples (type 0.005; precision 0.1°C; California Fine Wire, Grover City, Calif., USA) and stored on a data logger (Squirrel 1200 series; Grant Instruments, Cambridge, UK). Since the data logger had four operative input ports, one of the two combinations was recorded at the same time: (1) three egg-surface temperatures and one ground-surface temperature, or (2) three egg-core temperatures and one ground-surface temperature. We measured the temperature of the eggs before exposing them to sunlight to make sure that their starting temperatures were similar. The eggs were then exposed in the sun for approximately 2 h before we started recording. Winds were not so strong as to influence the results, but we stopped the experiment immediately when it clouded over or started raining.

During the temperature measurements, the eggs were placed on a ground surface that was similar to that of a natural Ostrich nest location, and its temperature was measured by placing a thermocouple on it. One brown-painted, one white-painted and one control egg were always measured at the same time. Thermocouples attached with transparent tape on top of the eggs were used to measure the surface temperature of the eggs on 2 days (5 and 6 December) between 1450 and 1610 hours, and the eggs were switched every half an hour. Egg-core temperatures were measured on 4 days (7, 10, 11 and 12 December), between 1230 and 1630 hours. To do this, a hole was drilled right at the centre of the egg and a stiff polypropylene tube (length 68 mm, outer diameter 3 mm, inner diameter 0.8 mm) carrying the thermocouple was inserted into the egg. This tube was mounted firmly at a 90° angle onto a plastic base (60 mm in diameter and 4 mm thick) which was sealed to the surface of the egg with epoxy glue.

Egg visibility

The visibility study was carried out on overcast afternoons so as to reduce any effect of sunshine reflecting from the painted eggs. Two eggs, one painted brown and one control, were placed beside a person, and the observer walked away from the eggs until they disappeared from her vision. Then she started walking towards them. When she saw the first egg, she immediately stopped and recorded the distance to the person beside the eggs using a Leica Geovid Rangefinder (7 × 42 BDA; accuracy: ± 1 m; Leica, Portugal). The observer then continued walking until she saw the second egg, and again recorded the distance to the person beside the eggs. The experiment was done repeatedly on different days and in different types of vegetation with different heights of grass.

Data analysis

The egg volume was calculated as volume (cm^3) = L × B^2 × 0.00051, where L is the length (mm) and B is the breadth (mm) of an egg (Hoyt 1979). Surface and core temperature data were recorded every minute during the experiments. In the subsequent analyses, we used only one value of temperature for every 0.5 h for each variable (eggs and ground). The 0.5 h temperature was calculated as the mean of the temperatures recorded during a 10-min interval (5 min before and after the 0.5 h time).

We measured the temperatures of six eggs (two brown-painted, two white-painted and two controls). To control for repeated measurements of each egg in the subsequent statistical analyses, we used a mixed linear model and entered egg identity as a random factor (Crawley 2002). The mixed linear model analysing the surface temperature of the egg was entered with the egg colour (factor: brown, white, control) and date (factor: 5, 6 December) and time of day (covariate) as explanatory variables. The model analysing the egg-core temperature was entered with the egg colour (factor: brown, white, control), date (factor: 7, 10, 11, 12 December), time of day (covariate) and the quadratic term of time of day (covariate). The model analysing the egg-core temperature was specified as an autoregressive model to control for the temporal autocorrelation within the time series of temperature measurements. Visibility between brown-painted and control eggs was compared using a paired sample *t* test. Statistical analyses were performed with S-PLUS v7.0 (Insightful, Seattle, Wash., USA). Means are reported with ± standard error.

Results

Egg-surface temperatures

The egg-surface temperature was significantly influenced by the colour and the date ($P \leq 0.001$; Table 1, Fig. 1). However, time of day had no significant effect as a covariate ($P = 0.12$; Table 1) because the experiment was conducted during a very short period of the day (between 1450 and 1610 hours). The surface temperature of the brown eggs was significantly higher than that of the white and control eggs ($P = 0.001$; Table 1, Fig. 1). The mean surface temperatures of the white and control eggs were 11.5°C (±0.78) and 10.8°C (±0.63) lower than the brown eggs, respectively. Since 6 December was significantly warmer than 5 December ($P < 0.001$; Table 1, Fig. 1), considerable variation is likely between different days.

Table 1 Summary of a mixed linear model analysing the surface temperature of Ostrich (*Struthio camelus*) eggs as a function of egg colour (brown, white or control), date and time of day on 5 and 6 December 2006

	Num *df*	Den *df*	*F*	*P*
Final model				
Intercept	1	15	15,391	<0.001
Egg colour	2	3	148	0.001
Date	1	15	182	<0.001
Rejected terms				
Time of day	1	15	2.7	0.12

Num *df* and Den *df* represent the numerator and denominator degrees of freedom, respectively

Egg-core temperatures

The core temperature of the eggs was found to be significantly influenced by egg colour, date, time of day, the quadratic term of time of day, and the interactions between egg colour × date, egg colour × time of day, and egg colour × quadratic term of time of day (Table 2). The mean core temperatures of the brown eggs were 11.3 and 10.1°C warmer at the hottest part of the day than the white and control eggs, respectively, . The core temperature of the brown eggs was significantly higher than that of the white and the control eggs ($P < 0.001$; Table 2). There was a tendency of gradual increase in the egg-core temperatures as a function of time, following a quadratic curve with an increasing difference between brown eggs and white and control eggs as the day progressed (Fig. 2). We have presented the predicted core temperatures of the

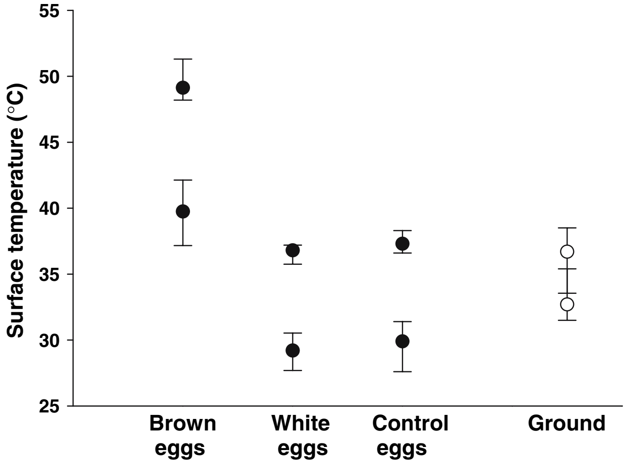

Fig. 1 Surface temperature (°C) of brown-painted, white-painted and control Ostrich (*Struthio camelus*) eggs, and the ground, measured between 1450 and 1610 hours on 2 days (5 and 6 December 2006). The *circles* represent the two mean surface temperatures of the 2 days, respectively, and the *error bars* represent the maximum and minimum temperatures recorded on the 2 days, respectively

Table 2 Summary of a mixed linear model analysing the core temperature of Ostrich eggs as a function of egg colour (brown, white or controls), date and time of day, on 7, 10, 11 and 12 December 2006

	Num *df*	Den *df*	*F*	*P*
Intercept	1	39	386,801	<0.001
Egg colour	2	3	2,490.9	<0.001
Date	3	39	428.4	<0.001
Time of day	1	39	4,240.8	<0.001
Time of day (quadratic)	1	39	168.4	<0.001
Egg colour × date	6	39	40.7	<0.001
Egg colour × time of day	2	39	133.8	<0.001
Egg colour × time of day (quadratic)	2	39	8.3	0.001

Num *df* and Den *df* represent the numerator and denominator degrees of freedom, respectively

experimental eggs (along with the predicted ground-surface temperature) for the warmest day (12 December) to illustrate the great effects of egg colour and to show the temporal pattern (Fig. 2). The predicted egg-core temperatures are derived from the parameter estimates obtained from the analysis in Table 2, whereas the predicted ground-surface temperatures are derived from parameter estimates from a linear model including "date" as factor and with "time of day" and the quadratic term of time of day as covariates. The core temperatures of the brown eggs exceeded 37.5°C, which is the temperature at which the mortality of Ostrich embryos starts to increase, whereas the core temperature of white or control eggs was below 37.5°C. The ground-surface temperature was highest at 1440 hours, whereas the egg-core temperatures were highest at 1655 hours, indicating a time lag for the core temperature of the eggs to be raised to the peak temperature.

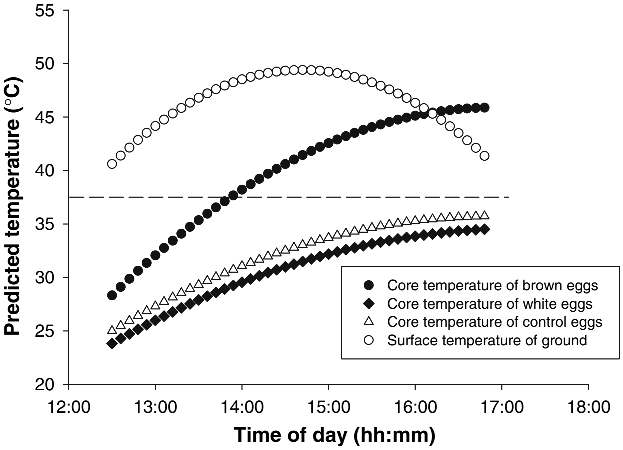

Fig. 2 Predicted core temperatures (°C) of brown-painted, white-painted and control eggs, and predicted surface temperature of the ground, as a function of the time of day on the warmest day of the measurements (12 December 2006). The predicted core temperatures for the warmest day are derived from the parameter estimates obtained from the analysis in Table 2. For the warmest day, the ground temperature = 53.5 × time of day −1.82 × (time of day × time of day) −343.6. The *dashed horizontal line* represents the egg-core temperature (37.5°C) at which embryo mortality starts to increase

Egg visibility

The mean discovery distance to the control egg from the observer was significantly longer than that of the brown-painted egg (control: 28.1 ± 3.9 m; brown: 17.3 ± 2.0 m: $t_{15} = -4.85$, $P < 0.001$). The scatter plot shows a linear relationship between the visibility of the white and brown eggs (linear regression: distance to brown-painted egg = 0.47 (± 0.06) × distance to control egg + 4.16 (± 1.8), $r^2 = 0.83$, $n = 16$, $P < 0.001$; Fig. 3), and the slope of this relationship was significantly different from 1 (the upper 95% confidence limit for the slope was 0.59), demonstrating a higher visibility of white eggs.

Discussion

There was a significant effect of egg colour on both the surface and core temperatures of the Ostrich eggs during exposure to direct sunlight, and egg temperatures varied substantially between different days. The effect of time of

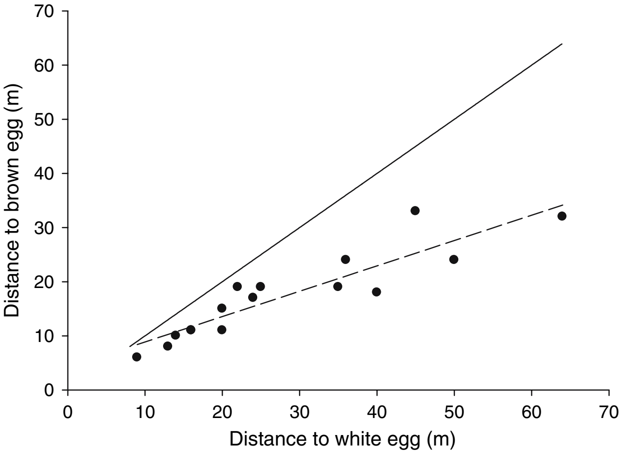

Fig. 3 Relationship between the visibility of brown-painted and control eggs for an observer walking towards the eggs. The *thick line* represents the 1:1 relationship between the distances to the brown-painted and control eggs. The *dashed line* represents the real relationship observed during the experiment in which the control egg was observed first

day with respect to surface temperature was not seen due to the short period of time in which the experiment was conducted (Table 1), but we assume that it follows the same temporal pattern as shown for the ground-surface temperature in Fig. 2. The egg-core and ground-surface temperatures showed a significant quadratic temporal pattern, with peak temperatures being obtained in the late afternoon (Fig. 2). Moreover, the significant interactions between egg colour × time of day, egg colour × quadratic term of time of day and egg colour × date demonstrate that the difference in core temperature between the different egg colours varied with the time of day and between dates. Thus, the core temperature of brown eggs was significantly higher than that of white-painted and control eggs, and the difference was highest in late afternoon and on the warmest day (Table 2; Fig. 2).

Since some types of egg pigments cause higher solar reflectance than others (Bakken et al. 1978), we regard the brown-painted eggs as crude representatives rather than perfect representatives for cryptic brown eggs in nature. However, the substantial differences in temperature between white- and brown-painted eggs demonstrated in this experiment suggest that egg coloration may have significant fitness consequences. On the warm and sunny days, the core temperature of the brown eggs was well above 40°C, whereas the white-painted and the control eggs were below 37.5°C. An estimate of the upper thermal tolerance for short-time exposure in most species is 41°C, and for exposures lasting several hours it is 39°C (Webb 1987). In Ostriches, increased embryo mortality is reported at temperatures above 37.5°C (Hassan et al. 2004; Ipek et al. 2003) and reduced hatching success is reported at temperatures above 40°C (Deeming et al. 1993). The high core temperatures of brown-painted eggs observed in this experiment (Fig. 2) would be lethal to Ostrich embryos given the Ostrich's habit of leaving the nests exposed to solar radiation during the day before the start of incubation. The warmest day on which we conducted the experiment had a maximum air temperature of only 30°C (G. Mwakalebe, Serengeti Meteorological Centre, personal communication), suggesting that the selection pressure against unattended brown eggs would be very high in excessive temperatures if brown Ostrich eggs existed in this environment. Therefore, white seems to be the adaptive Ostrich egg colour to prevent overheating (Bertram and Burger 1981).

Cryptic egg coloration could be explained as an adaptive anti-predator strategy in ground-nesting birds (Montevecchi 1976; Solís and de Lope 1995; Lloyd et al. 2000), although coloured eggs may impose a predation risk to some bird species, an idea for which there is support (Montevecchi 1976; Götmark 1992; Weidinger 2001). It has been argued that Ostriches lay white eggs because they are powerful enough to defend their nests (Wallace 1889). However, when nests are unattended, such big eggs are quite visible on the ground to both mammalian and avian predators. In our visibility study, a naturally white egg was seen first by the observer, suggesting that the brown eggs are better concealed. Ostriches would therefore have derived a selective advantage in the face of predators by having brown eggs. Our results therefore are consistent with the prediction, and support Bertram and Burger's (1981) conclusion, that white Ostrich eggs minimise overheating, but are prone to predation.

In conclusion, brown Ostrich eggs, if they had evolved, would have been less easily detected by predators than white eggs, as demonstrated by our visibility experiment. On the other hand, unattended brown eggs would be overheated on sunny and hot days, imposing a strong selection against brown eggs. Although some types of natural egg pigments may modify the degree of overheating, parent Ostriches could probably only leave brown eggs unattended on cold days or for very short periods of time (<1 h) on sunny and hot days without risking overheating. Hence, the strategy to leave the eggs unattended for several days before incubation starts only seems possible with white eggs.

Zusammenfassung

Die weiße Farbe der Eier vom Strauß (*Struthio camelus*) ist ein trade-off zwischen Prädation und Überhitzung

Die meisten Bodenbrüter legen pigmentierte Eier, und die Eipigmentierung ist generell der Umwelt angepasst. Pigmentierung von Eiern hat sich als Schutzmaßnahme gegen Prädation entwickelt, aber dunkel pigmentierte Eier können anfällig für Überhitzung sein, wenn sie der Sonnenstrahlung ausgesetzt sind. Der Strauß legt weiße Eier, die während der ersten Wochen vor Bebrütungsbeginn unbeaufsichtigt und recht gut sichtbar für Prädatoren sind. Um die Effekte der Farbe auf die Temperaturen an der Oberfläche und im Inneren der Eier abschätzen zu können, haben wir einige Straußeneier dunkelbraun oder weiß angemalt und einige als Kontrolle unangemalt gelassen und alle tagsüber direkt der Sonne ausgesetzt. Die Oberflächen- und Kerntemperaturen der braunen Eier waren signifikant höher als die der weiß angemalten Eier und Kontrolleier. Außerdem überstieg die Kerntemperatur der braunen Eier 37.5°C, diejenige Temperatur, bei der die embryonale Sterblichkeit zuzunehmen beginnt. In einem zweiten Experiment haben wir Eier (braun angemalte und Kontrolleier) in verschiedenen Vegetationstypen platziert, um ihre Sichtbarkeit für einen auf sie zugehenden Beobachter

zu untersuchen. Die weißen Eier wurden aus signifikant größerer Entfernung entdeckt als die braunen Eier, was darauf hindeutet, dass das Prädationsrisiko für weiße Eier deutlich höher sein dürfte. Die Ergebnisse lassen daher darauf schließen, dass weiße Eier Überhitzung minimieren und es dem Strauß erlauben, seine Eier vor Bebrütungsbeginn unbeaufsichtigt zu lassen, jedoch sind sie anfälliger für Prädation.

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PAPER III

Do ostriches (*Struthio camelus*) recognise their own eggs?

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Abstract

The ostrich communal breeding system involves several females laying in a single nest. However, only the ‘major’ female and the territorial male provide parental care from incubation to fledging of chicks. Eggs are turned and displaced frequently upon the onset of incubation, and the major female ejects excess eggs out of the nest when the number of eggs is above a specific threshold level. We assessed egg movement during the egg-laying stage based on photographs, and measured central incubated and ejected unincubated eggs by using ultraviolet-visible reflectance spectrophotometry in order to assess variation in colouration between eggs. There was no significant difference in the movement of eggs between central and peripheral nest layers. Furthermore, a binomial mixed model analysis revealed that central and ejected eggs did not differ in spectral reflectance. In addition, ejected eggs that were experimentally placed in the middle of the nest were not preferentially ejected once more (only 1 of 6 eggs was ejected). These results suggest a general trend of random movement of eggs in the nest, and furthermore that eggs are ejected more or less randomly. Therefore, there is no indication that the major female can precisely identify her own eggs and exclude others based on the appearance of eggs.

Introduction

Ostriches (*Struthio camelus*) are the largest extant flightless birds, found in a variety of open habitat types, avoiding areas of thick bush or heavy tree cover (Brown et al. 1982). Four ostrich subspecies are found in Africa (Brown et al. 1982, Bertram 1992), including the Masai ostrich (*S. c. massaicus*), which is the target of the present study. Generally ostriches are primarily polygynandrous with both sexes mating with multiple partners (Sauer and Sauer 1966, Bertram 1992, Kimwele and Graves 2003), and several females may lay in a nest (communal nesting) whereby the first female to lay is considered as the 'major' female and females that subsequently lay in the same nest are referred to as 'minor' females (Sauer and Sauer 1966, Hurxthal 1979, Bertram 1992, Kimwele and Graves 2003). However, in such a cooperative breeding, guarding and incubation of the nest is the responsibility of the major female during the day and the territorial male during the night (Bertram 1992, Kimwele and Graves 2003), though this rule is not invariable (Bertram 1992, own data).

The major female lays on average 11 eggs (range 8-16) (Bertram 1992), while one to seven minor females may lay 20-40 additional eggs in the nest, which is considerably in excess of the number that can be incubated (Sauer and Sauer 1966, Hurxthal 1979, Bertram 1992). The clutch size in ostrich nests before incubation may contain up to 30-40 eggs (Leuthold 1977, Bertram 1979). Laying of eggs by the major hen in a nest generally stops after the onset of incubation, although additional eggs may be laid by minor females (Bertram 1992). During laying period, both major and minor females have a tendency to lay in the middle of the nests (own observation), however at the onset of incubation, eggs are turned and moved from one position to another to stimulate embryo growth (Hallam 1992, Deeming 1997), therefore allowing mixing and movement of eggs between layers in the nest. The average incubation period for ostriches is 42 days (Bertram 1992).

Egg-laying by minor females can be regarded as cases of intraspecific brood parasitism, which has been reported to occur mainly among colonially breeding birds (Yom-Tov 2001) and precocial birds (Yom-Tov 1980, 2001, Bertram 1992). Generally, brood parasitism is disadvantageous to the host female in terms of fitness costs (Andersson 1983, Bertram 1992, Lyon 2003). Studies on interspecific avian brood parasitism have obtained support for that egg discrimination by hosts is a coevolved anti-parasite strategy (e.g. Davies and Brooke 1989, Moksnes et al. 1990, Rothstein 1990). Lyon (2003) found that American coots (*Fulica americana*) are able to recognize and reject eggs laid parasitically by conspecifics. In addition, experimental studies have shown that several passerines are able to recognize and reject a range of conspecific eggs (e.g. Welbergen et al. 2001, Procházka and Honza 2003, 2004, Avilés 2004, Honza et al. 2004, Stokke et al. 2004, Antonov et al. 2006a, b). Visual cues are of critical importance to hosts in discriminating between their own and foreign eggs (e.g. Brooke and Davies 1988, Davies and Brooke 1988, Stokke et al. 1999, 2005).

Lack (1947), documented that clutch size in some precocial species has an upper limit set by the incubation capacity of the parent ('the incubation capacity hypothesis'). Therefore, at the start of incubation, the major female arranges the eggs into a central, incubated clutch and a ring of peripheral, unincubated eggs (Kimwele and Graves 2003). Since major female and territorial male ostriches are only able to incubate about 20-21 eggs (Hurxthal 1979, Bertram 1979, 1992), some excess eggs are ejected by the major female 1-2 metres away from the nest where they remain unincubated and will never hatch (Sauer and Sauer 1966, Bertram 1979, 1992). Bertram (1979, 1992) argued that major ostrich females benefit from extra eggs against predation through dilution in the nest (retention of some eggs in case of partial nest destruction) and dilution of chicks (protection gained when chicks join with others), indicating that host females should accept parasitic eggs to some extent. Therefore, acceptance of parasitic eggs can be optimal as long as the number of eggs is below a certain threshold level and rejection costs are high (Bertram 1979, 1992, Davies et al. 1996, Røskaft et al. 2002, Stokke et al. 2002).

Risk of committing errors in recognition and rejection of foreign eggs are especially prominent when contrast between host and parasitic eggs is low (Stokke et al. 2005, 2007). Ostrich eggs are immaculate creamy white, which makes it difficult for the human eye to note differences in colour between them. However, Bertram (1979, 1992) indicated that major ostrich females recognise their own eggs based on eggs size, shape and surface texture relative to their own eggs. Furthermore, it might be that ostriches use variation in egg reflectance not detectable to humans in order to recognize foreign eggs in their nests. Most birds are sensitive to ultraviolet wavelengths (325-400 nm), to which humans are blind (reviewed by Bennett and Cuthill 1994, Bennett et al. 1994, see also Kawamura et al. 1999). Birds have at least four spectrally distinct cone types (Bowmaker et al. 1997), as opposed to three in humans, implying that birds probably have tetrachromatic, and even possibly higher dimensional, colour vision (Bennett et al. 1994). Avian cone cells contain light-absorbing oil droplets, which act as cut-off filters, reducing the overlap between cone spectral sensitivities (Bowmaker 1991, Vorobyev et al. 1998). Due to these differences between human and avian vision, several recent studies have made use of spectrophotometry when investigating features of avian eggs (e.g. Starling et al. 2006, Avilés et al. 2006, 2007, Cherry et al. 2007a,b).

Eggs of different ostrich females may possess different reflectance spectra perhaps due to genetical or environmental factors (see e.g. Avilés et al. 2007). Therefore, discrimination of minor females' eggs by major females may be performed based on differences in certain combinations of wavelengths. To investigate this possibility we compared spectral reflectance in the interval 325-700 nm of accepted and rejected ostrich eggs within single clutches. If ostrich females are able to recognize their own eggs, we expect differences between accepted (inner) and ejected eggs, and therefore we predict that, (a) eggs are moved non-randomly between inner and outer positions as the egg laying or incubation is progressing, (b) ejected eggs moved experimentally into the inner part of the nest would be ejected once more, and (c) ostriches recognise their own eggs by means of egg spectral reflectance, so that the eggs that remain in the nest (accepted and considered as major female eggs) deviate from the ones that are ejected (considered as minor female eggs) in reflectance.

Materials and methods

The study was carried out in the Serengeti National Park (SNP) in Tanzania (14,763 km^2) between October and December 2006. During the study, most ostrich nests were found in plain grasslands, their preferred habitat (Bertram 1992). Due to strict regulations of the SNP, we could not mark the females so as to identify the major and minor females. We only considered majority of eggs in the centre of the nest to belong to the major female and most of the rejected eggs minor females'. A total of 24 nests were found, and the clutch sizes were categorised according to Bertram (1992), i.e. small (1-10 eggs), medium (11-20 eggs) and large (21-30 eggs). All eggs in these nests were marked by numbering them using a water proof marker pen. In this study, we only considered large nests (N = 8), since ejection of the eggs frequently occur only in nests with more than 20 eggs (Bertram 1992). The reason for the small sample size is that most of the nests found were predated before experiments were terminated. The patterns of egg movements in the nests were documented at each visit by taking photos with a digital Hewlett-Packard (hp) camera (R707, 5.1 MP). Each time we visited the nests we turned the eggs so that the numbers were pointing up since some of the eggs were turned around in the course of incubation and thereafter we took photos. The photos were subsequently analysed to reveal if eggs had been moved from their original position or not. We classified three nest layers; eggs that were in the centre of the nest were considered as being in the inner layer and those in the periphery of the nest were considered to be in the outer layer, while unincubated eggs pushed out of the nest were regarded as rejected (Fig. 1).

To minimize disturbance, nests were visited once to twice a week during egg laying and incubation period. At the first visit, we obtained reflectance values of two eggs in the middle and one or two rejected eggs (if more than one egg were rejected) from all experimental nests with rejected eggs (N = 6) by using UV-visible reflectance spectrophotometry. Consequently, analyses were based on 12 middle and 10 rejected eggs. Furthermore, after spectrophotometric measurements were taken, one of the rejected eggs were randomly chosen and placed in the middle of the nest so that we could monitor if the egg was rejected once more.

Reflectance spectra in the range 325-700 nm were obtained from experimental eggs using a spectroradiometer (Ocean Optics, Europe) measuring at 0.37 nm intervals. Colour was measured once on three selected approximately 1 mm^2 areas of the surface of the eggs; in the pointed and blunt ends and in the middle of the egg. Two illuminants were used, i.e. deuterium and halogen light source (DH 2000). The light was transferred to the eggs through a quartz optic fibre (Ocean Optics) probe that reached the eggs at an angle of 45º from the light source and transferred reflected light to the spectrometer. Data from the spectrometer were passed into a computer, where a software package (OOIBase 32) calculated reflectance spectra relative to a standard white reference (WS-2) and to darkness. A reference and dark calibration were made prior to the measurement of each clutch. Reflectance at 0.37 nm was transformed to 1.11 nm intervals by calculating mean value for the three adjacent measurements. The mean reflectance spectrum for each egg in a clutch was calculated from the three spectra taken for each egg.

Statistical analyses

Movement of eggs between nest layers was analysed by performing chi-square tests. Eggs that were originally found rejected (third layer) were excluded from these analyses, since such eggs were subsequently never moved to another layer.

Principle component analyses (PCA) were used to describe reflectance spectra, in which the wavelengths and their corresponding reflectance values are reduced to a small number of variables (Cuthill et al. 1999, Cherry and Bennett 2001). We performed a PCA on the reflectance data set (i.e. reflectance at all 1.11 nm intervals between 325 and 700 nm) to minimize number of variables into four principal components (PCs) summarizing colour variation (Cherry and Bennett 2001). Principle components obtained from reflectance spectra on natural objects describes both achromatic and chromatic variations. The first principal component accounts for as much of the variability in the data as possible, and each succeeding component accounts for as much of the remaining variability as possible (Endler and Théry 1996, Cuthill et al. 1999). The first principle component (PC1) describes variation in mean reflectance (brightness, 'achromatic'), whereas PC2, PC3 and PC4 represent variation in spectral shape and therefore describes colour (chromatic) variation and saturation (Endler and Théry 1996, Cuthill et al. 1999). Differences in PC1, PC2, PC3 and PC4 scores were used as phenotypic egg matching measures between rejected and middle (inner) eggs within a clutch. The degree of consistency of reflectance data in our study was tested by the means of repeatability analyses (Falconer and Mackay 1996). Repeatability of colour estimates from the three measurements of each of the 22 selected eggs was calculated, and the repeatability was high (PC1: $r = 0.76$, $F_{21,65} = 10.50$, $P < 0.0001$, PC2: $r = 0.95$, $F_{21,65} = 52.41$, $P < 0.0001$, PC3: $r = 0.78$, $F_{21,65} = 11.40$, $P < 0.0001$, PC4: $r = 0.82$, $F_{21,65} = 14.97$, $P < 0.0001$). Consequently, all measurements were reliable and thus we used mean values for each egg. Possible differences in egg colouration between rejected and middle eggs in the nests were studied by a binary mixed model procedure. In the model we entered clutch identity as a random factor, whereas the independent variables PC1, PC2, PC3 and PC4 were entered as fixed factors. Means are reported with ± standard error. All analyses are two-tailed and were carried out in R 2.5.1 Software (R Development Core Team 2007).

Results

Egg movements

Number of eggs in the nest at the onset of incubation was 29 ± 2 eggs (range 23-38, N = 8), and the overall mean number of rejected eggs was 3 ± 1.2 eggs (range 0-9, N = 8). Mean number of rejected eggs in nests where at least one egg was ejected was 4 ± 1.4 eggs (range 1-9, N = 6). From the analysis of nest photographs (N = 8), and excluding eggs that were originally found in the third layer (see methods above), we found no significant difference in movement of eggs from their original position between the three nest layers ($\chi^2 = 0.05$, df = 2, P = 0.98). In addition no significant difference was observed in movement of eggs within nests (Table 1). Eggs that were ejected out of the nest were generally not moved back into the nest by the host (except a nest where one egg was originally found in the inner layer, then it appeared in the third layer, but finally it was taken back to the inner layer of the nest). Experimental eggs that were originally rejected and put in the centre of the nest were as well moved randomly from one point of the nest to another and only one egg was rejected out of the nest once more (Table 2). The table shows the number of days the experiment was monitored, before the nest was deserted or predated.

Spectrophotometric differences between rejected and inner eggs

The principle component analysis allowed us to differentiate between achromatic variation described by the first principle component (PC1) and chromatic variation represented by PC2, PC3 and PC4 between two randomly selected inner and one or two rejected eggs. The first four principal components together explain 97.8 % of the variance in spectra (Fig. 2). PC1 explains 71.6 % of the variance, is flat from 400 nm and had positive loading at all wavelengths, and as a result represents brightness (achromatic) variation. Other principal components (PC2, PC3 and PC4) were not spectrally flat (Fig. 2) and so represent aspects of the eggs' chromatic (colour) variation and together explained 26.3 % of total variance (16.6 % can be attributed to PC2, 8.9 % to PC3, and 0.8 % to PC4). However, there was no significant difference in any of the principal components between inner and rejected eggs, although there was a trend towards that they differed in reflectance in the yellow-green part of the spectrum (i.e. PC4, Table 3).

Discussion

Three lines of evidence from the present study indicate that major female ostriches are not able to distinguish own eggs from those of minor females. Firstly, eggs were moved randomly between nest positions during egg laying and incubation. During egg-laying and incubation, eggs are turned and moved to stimulate embryo growth, ensure uniform temperature and avoid sticking of the embryos on the egg shell wall (Hallam 1992). In the process of egg movement, eggs are moved from inner to outer layers and vice versa. Since more eggs are laid than can be incubated, the major females should get rid of excess eggs through ejection in order to increase the hatchability (Wilson et al. 1997, Anold 1999, Fernández and Reboreda 2007). In the present study, eggs ejected from the nest were generally left there and not moved back again into the nest, supporting findings from previous studies (Sauer and Sauer 1966, Bertram 1979, 1992). However, there was a case where one egg was ejected from the nest, but a few days later reappeared in the nest. Since laying females were not marked, it is difficult to tell whether it was a major or minor female that brought the egg back to the nest. However, Bertram (1992) asserts that it is the major females that moves the eggs around and not the minor females nor the territorial male, meaning that the rejected egg probably was brought back into the nest by the major female. Furthermore, there was no significant difference in the movement of eggs between the inner and outer layer of the nest suggesting that movement of eggs in the nests is more or less random without any clear pattern.

Secondly, rejected eggs moved experimentally into the inner part of the nest were generally not rejected again; only one egg was ejected out of the nest once more while the remaining eggs were apparently accepted. If ostriches were able to distinguish between own and foreign eggs, the experimental eggs should subsequently be ejected from the nest.

Thirdly, rejected and accepted eggs did not differ significantly in spectral reflectance. In the best of our knowledge, this is the first study of egg colouration in ostriches using reflectance spectra over the birds' visible range (i.e. 325-700 nm). We found no difference between accepted and rejected eggs in any of the principal components representing achromatic and chromatic variation, although PC4 showed a trend towards difference between the accepted and rejected eggs where the latter reflected less in the yellow-green part of the spectrum.

All these findings combined, reveal that ostriches apparently do not recognize their own eggs as it has been observed in other communally-laying species (Bruning 1974, Vehrencamp 1977), and furthermore that major females do not reject parasitic eggs selectively. Therefore, our findings do not support Bertram (1979, 1992) in that major females selectively rejected minor female's eggs. Ostrich eggs laid by different females appear to be very similar in appearance, and it is apparently difficult for major females to differentiate own eggs from those of minor females. Therefore, parasitic eggs are accepted because they fall below the cognitive threshold for recognition (see Rodriguez-Girones and Lotem 1999, Stokke et al. 2005, 2007, Hauber et al. 2006). Our results are in accordance with other studies on birds laying more or less immaculate eggs (Moksnes and Elvertrø 2006, Siefferman 2006, Underwood and Sealy 2006). Species with maculate eggs, however, are often able to recognize and reject conspecific eggs as long as they are contrasting somewhat in appearance from own eggs (e.g. Welbergen et al. 2001, Procházka and Honza 2003, 2004, Avilés 2004, Honza et al. 2004, Stokke et al. 2004, Antonov et al. 2006a, b, but see Antonov et al. 2006c).

Results from a recent molecular genetic study (Kimwele and Graves 2003) provided support for Bertram's (1979, 1992) findings that ostriches recognize their own eggs, because major females incubated more of their own eggs than would be expected if they were incubating all eggs at random. We have to bear in mind that the sample sizes in both our study and the one by Kimwele and Graves (2003) were low. Based on the findings from the present study, it is difficult to see how ostriches should be able to recognise their own eggs when both assessments based on human vision and spectrophotometric measures do not find significant differences between eggs apparently laid by several ostrich females. When eggs are very similar in appearance with extremely low variation between individual females, it is hard to find theoretical support for the hypothesis that female ostriches should be able to recognise their own eggs. This is because, among brood parasitic hosts, where the costs of accepting alien eggs are much higher than the assumed costs in ostriches, it is extremely rare that hosts recognise eggs that are similar to their own ones, as is the case of the immaculate ostrich eggs (see Stokke et al 2004, 2005). Thus there is little theoretical and experimental support for Bertram's (1979, 1992) hypothesis. However, clearly, more studies are needed in order to further reveal the generality of our findings.

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Table 1. Movement of ostrich eggs among nest layers (inner, outer, and rejected layer) from their original position during the egg laying period. df = 1 for nests with eggs moved only between inner and outer layer, whereas for nests with eggs moved among inner, outer and rejected layers df = 2. N = number of eggs in a nest.

Nest	N	Pearson Chi-square	df	P
1	23	0.69	1	0.41
2	23	1.66	2	0.44
3	25	1.00	2	0.61
4	28	0.45	1	0.50
5	30	1.19	2	0.55
6	30	3.24	1	0.07
7	33	3.65	1	0.06
8	38	0.65	1	0.42

Table 2. Movement of originally rejected ostrich eggs that were experimentally placed in the centre of the nest.

Nest	Observation days	First observation	Final observation
1	8	Inner layer	Outer layer
2	11	Inner layer	Inner layer
3	9	Inner layer	Outer layer
4	14	Inner layer	Inner layer
5	55	Inner layer	Inner layer
6	4	Inner layer	Rejected

Table 3. Parameter estimates with standard errors (SE) and test statistics for independent fixed variables entered into a binary mixed model explaining variation in eggs found inside or outside ostrich nests (N = 6). PC1 indicates principal component 1, PC2 principal component 2, PC 3 principal component 3 and PC4 principal component 4.

	Estimate	SE	Z value	P
Intercept	-0.34	0.51	-0.67	0.50
PC1	-0.87	0.63	-1.38	0.17
PC2	0.86	0.68	1.26	0.21
PC3	-0.20	0.55	-0.37	0.71
PC4	-1.10	0.58	-1.89	0.06

Figure legends:

Fig. 1. Graphical presentation of an ostrich nest with three layers showing central (inner) layer, peripheral (outer) layer and layer with excess rejected eggs.

Fig. 2. Factor loadings in relation to wavelength, derived from reflectance spectra from inner (N = 12) and ejected (N = 10) ostrich eggs (Number of clutches = 6). Curve colours are representing PC1 (blue), PC2 (green), PC 3 (grey) and PC4 (violet). PC1 represents brightness (achromatic) variation. PC2, PC3 and PC4 represent chromatic variation (for further information, see text).

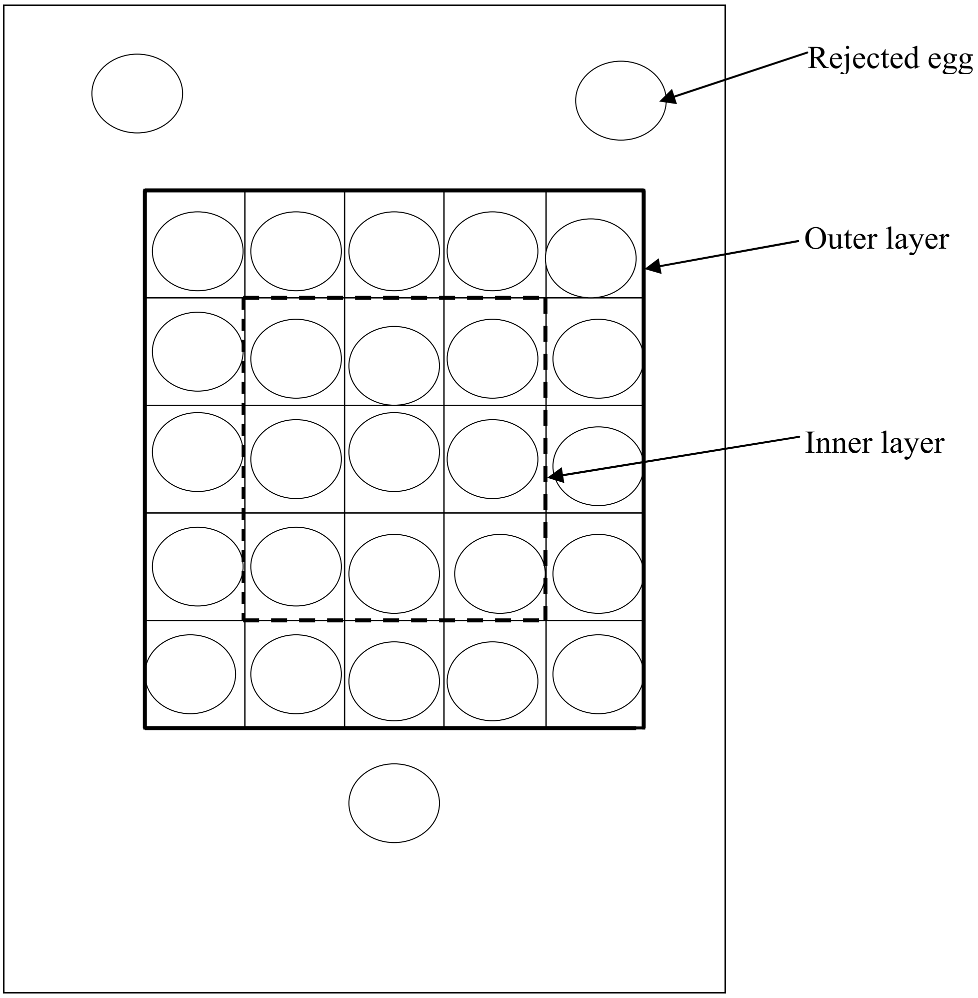

Fig. 1.

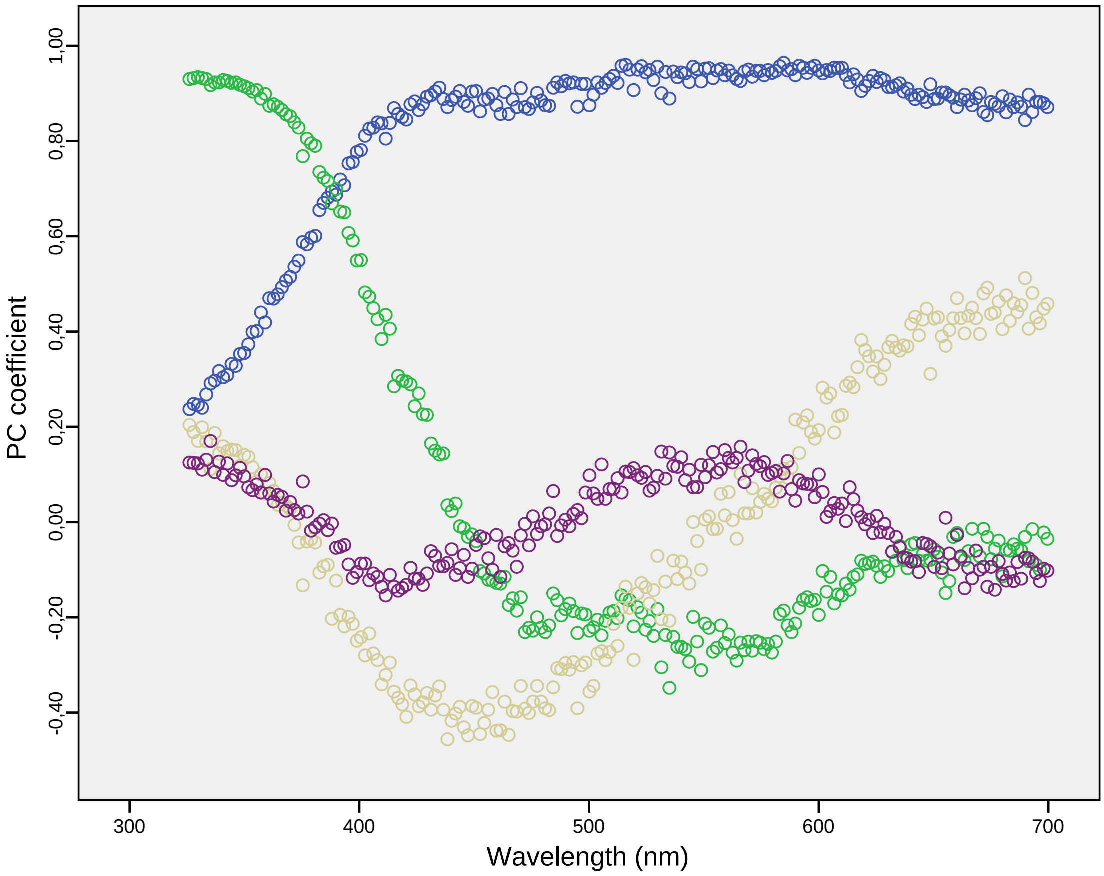
PC coefficient
1,00
0,80
0,60
0,40
0,20
0,00
-0,20
-0,40
300
400
500
600
700
Wavelength (nm)

Fig. 2.

PAPER IV

Running page heading: *Sex Ratio and Group Dynamics in Ostriches*

SEX RATIOS AND GROUP DYNAMICS IN OSTRICHES (*Struthio camelus*) IN THE SERENGETI ECOSYSTEM, TANZANIA

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ABSTRACT.–Ostriches (*Struthio camelus*) are poorly studied in the wild. They are commonly found in open habitat types. Males practising a territorial behaviour. During January 2005-December 2006, data was collected along 388 km of roads in Serengeti Ecosystem. Two areas, i.e. Serengeti National Park (SNP) and adjacent game reserves and open area (GR/OA), were compared with respect to ostrich sex ratios (female/female+male) and group sizes. Repetitive sampling revealed female-skewed sex ratio in the ecosystem. The sex ratio was significantly more skewed towards females in SNP than in GR/OA. In addition, sex ratios differed significantly between seasons, with a more female skewed sex ratio during dry than during wet season. The average group size was 3.0 ± 3.7 (SD) birds, with 85.1 % of the groups having one to four birds. There was no significant difference in group sizes between SNP and GR/OA, or between habitat types. However, temporal differences were observed, with significantly larger group sizes in wet than in dry season. Single males were observed more frequently during dry season. The ratio of male/other groups (other groups include single females or a mixed group) was significantly higher in dry than in wet season. This can be accredited to the breeding season which takes place during dry season where males become territorial. However males are exposed to high predation risk being solitary. In addition, ostriches commonly occurred singly, but the most common group composition was one male and one female both in the SNP and GR/OA. The sex ratio peaked as the group size increased. Female skewed sex ratio can be explained by differential mortality between sexes associated with male's behavioural traits. Variation in group size could be attributed to seasonal changes related to availability and quality of food together with natal recruitments.

Keywords: group size, ostrich, predation, Serengeti, sex ratio, *Struthio camelus*

INTRODUCTION

Parents divide their reproductive effort into the production of sons and daughters. The explanation for variation in sex ratios at birth is ingrained on relative profitability of raising sons and daughters between individual parents (Trivers and Willard 1973). Regardless of the mechanisms based on sex determination, males and females are produced in approximately equal numbers in most species (Fisher 1930, Bull and Charnov 1988, Edward 1998, Seger and Stubblefield 2002). Offspring sex ratio in wild bird populations, and the extent to which they vary from the equality expected by random genotypic sex determination have received much recent attention (Frank 1990; Sheldon 1998, Hardy 2002, Ewen et al. 2004). The success of sex allocation models in predicting sex ratios has been cited as one of the crowning achievements of evolutionary ecology, although its success in some vertebrates, particularly birds appears more modest (Sheldon 1998, West et al. 2002, Ewen et al. 2004).

In birds, imbalanced sex ratio skewed towards males is commonly related to physiological or behavioural traits (Mayr 1939). Female skewed adult sex ratio, frequently occurring in mammals (Fischer and Linsernmair, 2002; Holland et al. 2002; Setsaas et al. 2007), does not happen often in birds (Donald 2007). Female skewed adult sex ratios in birds can occur in species that exhibit polygynous (harem) behaviour (e.g. ostrich, *Struthio camelus*) or species exhibiting socially monogamous mating systems with high female parental care (Donald 2007).

In birds, there are several reports of sex ratio adjustment in relation to parental or environmental quality (Daan et al. 1996, Kilner 1998). Sex ratios are therefore likely to change if the populations are strongly subjected to factors such as predation and trophy hunting (Donald 2007). However, little is known about the patterns of natural variation in adult sex ratios, which is strictly defined as the sex ratio of breeding adults and commonly measured as the sex ratio of all independent non-juvenile individuals (Mayr 1939).

Few data exist on the biology of wild ostriches (Sauer and Sauer 1966, Jarvis et al. 1985, Bertram 1992). Native to Africa, this species is found in a variety of open habitat types (Brown et al. 1982), avoiding areas with thick bush or of heavy tree cover. Semi-arid, open and short grass plains are usually associated with high densities of ostriches. Ostriches tend most often to be solitary birds or in pairs, whereas large social groups, usually consisting of females, are less frequent (Bertram

1992). However, formation and splitting of groups occurs frequently (Roberts et al. 1970, Bertram 1992).

In previous studies, a female-biased adult sex ratio in ostriches has been reported in the national parks (Sauer and Sauer 1966, Hurxthal 1979, Bertram 1992). Differential male mortality (Bertram 1992, Donald 2007) following male solitarily behaviour (Bertram 1992) suggest male territorialism. Male ostriches occupy a territory with an average range of 16 km^2, particularly during the breeding season (Bertram 1992). Nevertheless, males are known to form social groups outside the breeding season (Sauer and Sauer 1966, Bertram 1992). Seasonal changes, quantity and quality of food may influence distribution and grouping of animals (McNaughton and Georgiadis 1986, Skarpe and Bergström 1986).

None of the previous studies in ostriches compared demographic variations between national parks and partially protected areas. Partially protected areas (IUCN category ≤ IV) (UNEP-WCMC 2005) function as buffer zones to protected areas in eastern and southern Africa, and usually allow some kind of consumptive use of natural resources within their boundaries. In the Serengeti ecosystem, partially protected areas are heavily impacted by an increasing human population and illegal hunting (Campbell and Borner 1995; Hofer et al. 1996). Several studies indicate that wildlife exploitation alter demographic dynamics (Herremans 1998, Ostrowski et al. 2001, Sinclair et al. 2002, Thiollay 2006). In this study we compared the variables ostrich sex ratio, group size and group composition between national park and partially protected areas, in addition we compared the variables with respect to seasons i.e. wet and dry season.

Although hunting of ostriches is restricted in protected areas, interviews with local residents suggest that illegal hunters frequently visit partially protected areas and sometimes even the national park. There they use both active hunting methods as well as unselective wire snares to kill ostriches (Holmern et al. 2006, F. Magige et al. unpublished data). Hunters in this area frequently target males (Holmern et al. 2006) which may cause demographic changes in terms of female skewed sex ratios. In addition, the reaction of birds to human approaches can be equated to the perceived threat of predation (Lima and Dill 1990), since wildlife reacts to humans and predators in similar ways (Frid and Dill 2002). Therefore, birds are expected to form large groups in partially protected areas as a means of anti-predator defence.

The aim of this study was to compare the spatial and temporal sex ratios and group sizes of ostriches in the Serengeti National Park and adjacent partially protected areas. We specifically analysed whether: (1) adult sex ratios varies with area (2) adult sex ratios varies with season, (3) group sizes varies with area, (4) group size varies with season, (5) frequency of single adult males varies with seasons and (6) group composition varies with group size.

METHODS

*Study area.–*The study was conducted in Serengeti National Park (SNP) (14,763 km^2) and adjacent partially protected areas i.e. Ikorongo (563 km^2) and Grumeti (416 km^2) Game Reserves and Ikoma Open Area (600 km^2) collectively abbreviated as GR/OA, Northern Tanzania (Fig. 1). The study was carried out between January 2005 and December 2006. In this area there are mainly two seasons, a wet season recorded from November to May and a dry season from June to October (Norton-Griffiths et al. 1975). The mean annual rainfall varies from 800 mm in the eastern to 1,050 mm in the northern part of the study area (Campbell and Hofer 1995). In the south, there are short and long grass plains, an extensive block of acacia savannah woodland is found at the centre. The western corridor, which extends up to the edges of Lake Victoria, is a region of wooded grassland and woodlands dominated by *Acacia* species.

Sex identification and group size.– Different parts in the SNP and GR/OA were visited once a week, and data collection normally began at 08:00 and ended approximately 06:00 pm. Data was systematically collected on observations of ostriches along established road networks covering a total length of 388 km. Average length of the road was 77.6±44.8 (SD) km (range = 30-145 km). The observations were usually made by two people within 1 km on either sides of the road in an open roofed vehicle at a speed of 20-40 km/h, with some frequent stops for scanning. When a group of ostriches was sighted, the group size and composition were determined using a Leica Geovid rangefinder (Leica, Portugal; 7x42 BDA accuracy: ± 1 m). Group size was estimated using all the visual observations (which could have included repeated observations of the same group of birds in different days). Birds observed within 100 m of each other were regarded as one observation. We also recorded sex of the adult birds, vegetation type and age (adult > 2 years, juveniles < 2 years or chicks < 3 months). Vegetation was categorised according to Kikula (1980) and Caro (1999), but because of small sample size we pooled habitat types into two categories; closed habitat (woodlands and bushlands) and open habitat (grasslands, wooded grasslands, bushed grasslands and cultivated lands).

We were unable to sex juveniles and chicks, therefore, such individuals were excluded from the sex ratio analysis. Male and female juvenile/chicks are very similar in appearance and their sex can only be determined by examining their sexual organs, though this examination can still be difficult (Samour et al. 1984, Gandini and Keffen 1985). Full distinction between sexes is reached at about two years of age. The adult male's body plumage is jet black, with exception of a white plumage on its wings and tail whereas female's feathers are of fairly uniform earthy pale brown-grey colour (Bertram 1992).

Since ostriches prefer open habitat types, they were frequently and easily observed in these habitat types even beyond 1 km. However, in dense vegetations like bushed and wooded grasslands ostriches might have been overlooked, due to reduced detectability. Single individuals even at distances of a few hundred meters might not be detectable; suggesting that habitat related differences in bird detectability might have slightly influenced the results.

Statistical analyses.–Variations in adult sex ratios (expressed as females/females+males) in both areas was determined. Records of sex ratios were averaged across the years and seasons. Differences in sex ratios between areas and seasons were tested with One-Way analysis of variance (ANOVA), where area (i.e. SNP and GR/OA) and season (dry and wet) were incorporated as random factors, respectively. Average group size was calculated as total number of ostriches observed divided by number of observations. We also determined the differences in group sizes between, areas, seasons and habitat types by One-Way Analysis of variance (ANOVA) where area, season and habitat type were entered as random factors, respectively. To test for habitat differences in group size, this variable was categorized according to the habitat where the group was observed, and compared between habitat types. Chi-square tests were used to test the frequency of single males compared to other groups (i.e. single females or groups of more than one individual) between wet and dry seasons. SPSS 12 was used for all analyses. Significant level was set at 0.05. Values are presented as mean ± standard deviation.

RESULTS

Sex ratio.–We recorded a total of 2485 ostrich observations. Most ostrich observations (73%) were in open grasslands. The overall sex ratio (female/female+male) was found to be female biased (0.72). When the two areas were compared, the sex ratio in SNP was 0.72 and GR/OA was 0.62, and the difference was statistically significant ($F_{1,1723} = 19.3$, $P < 0.001$). In addition, in dry season the sex ratio was significantly more female skewed (0.75) compared to wet season (0.67) ($F_{1,1723} = 41.11$, $P < 0.001$).

Group size.– Using the total number of observations ($n = 2485$), the average group size was 2.95 ± 3.65 birds (range = 1 – 59, median = 2.0), with 85.1 % of the observations corresponding to groups of one to four birds. However, there was no significant difference in groups size between SNP (2.94 ± 3.70 birds) and GR/OA (3.06 ± 3.06 birds) ($F_{1,2483} = 0.18$, $P = 0.67$). There was a significant decrease of group size in dry season (2.56 ± 3.30 birds) compared to wet season (3.51 ± 4.04 birds) ($F_{1,2483} = 41.40$, $P < 0.001$). The majority of groups were observed in the open habitat types (N = 2438 groups), approximately 98 % of the all observations made. However, there was no significant difference in group size between open (2.95 ± 3.64 birds) and closed (3.00 ± 4.38 birds) habitat types ($F_{1,2483} = 0.009$, $P = 0.93$).

The most common group sizes were one (38.6 % of groups), two (25.6 %), three (13.2 %) and four (7.7 %) individuals. In addition, there were 0.4 single male observations (N = 399) per other groups (N = 1059) in the dry season, compared to 0.2 single male observations (N = 202) per other groups (N = 825) in the wet season. The difference was statistically significant ($\chi^2 = 19.47$, df = 1, $P < 0.001$), indicating male solitarily and territorial behaviour during dry season.

For a total of 2423 groups for which sex/age could be determined, several types of group composition were observed (Fig. 2). The most common composition in SNP was one male (25.1 % of groups), followed by one male and one female (17.5 %) and one female (14.8 %). In the GR/OA, the pattern was similar with one male (26.0 %), followed by one male and one female (17.0 %) and one female (9.6 %), larger groups of adults were rare. In addition, both the number of male and female birds increased with group size, although the latter increased faster than the former (Fig. 3). As a result, sex ratio peaked from group sizes of four.

DISCUSSION

Sex ratio.–Our results revealed an overall female skewed sex ratio. The skewed sex ratio among adult ostriches appears to be a common phenomenon, as it has been observed in previous studies (Sauer and Sauer 1966, Hurxthal 1979, Bertram 1992). The results showed a skewed female sex ratio both inside SNP and GR/OA, although the sex ratio was highly skewed in SNP. The sex ratio also varied seasonally, with a higher skew towards females in the dry season compared to the wet season. Since most of solitary individuals are likely to be males, it could be the consequence of differential mortality between the sexes in relation to their grouping behaviour (i.e. solitary individuals could be more vulnerable to predation; see Bertram 1980, 1992). There are many cases where populations are regulated by predators (Sinclair et al. 2000, Sinclair et al. 2003). The main ostrich predators are lions (*Panthera lion*) and hyenas (*Crocuta crocuta*) (Kruuk 1972, Schaller 1972, Bertram 1992), although cheetahs (*Acinonyx jubatus)*, leopards (*Panthera pardus)* and wild dogs (*Lycaon pictus*) can be a threat as well (Sinclair et al. 2003). Most large predators are confined to protected areas, or in regions remote from human activities (Nowell and Jackson 1996, Nyahongo 2004, Packer et al. 2005). Ostrich predation is therefore likely to be high in the national park. Moreover, dry season coincides with ostrich breeding season, when male ostriches become territorial and hence more vulnerable to predation. We recorded two male ostrich carcases in central Serengeti with lion foot prints nearby (F. Magige and R. Sortland, personal observations), an indication of lion predation. Other records of lion predation are also available (Pienaar 1969, Schaller 1972, Rudnai 1974). Although sex ratios might be explained by predation, other variables such as hunting, egg collection might be important determinants of this variable.

Group size.– Results of a previous study on ostrich group size (see Bergström and Skarpe 1999) obtained an average of 5.0 birds along the year in Botswana, a value much higher than the value estimated in the present study of approximately 3.0 individuals in a group. However, the most common group sizes were those with one or two ostriches, large groups were quite rare, a pattern that has also been recorded by other authors (e.g. Roberts et al. 1970, Bertram 1992). There are advantages of living in groups, such as protection from predators, improvement of foraging, and efficiency of energy expenditure (Bertram 1980, Hammer and Parrish 1998).

Living in groups reduces the risk of predation through dilution (Hamilton 1971) and detection effects (Pulliam 1973). Due to increased human disturbance (e.g.

illegal hunting) in the partially protected areas, it was expected to find larger group sizes in these areas than in the national park. Non significant difference between these two areas with respect to group size indicates that ostriches do not respond to increased hunting pressure by increasing group size. Nevertheless, partially protected areas contain similar habitat types as in SNP (Herlocker 1976), this could probably create equally suitable environment for ostriches.

The general group size, as well as the tendency for larger groups to be formed during the wet season support results from other studies (Nagy and Knight 1994, Bergström and Skarpe 1999). Outside the breeding season, ostriches are known to be more gregarious (Bertram 1992), an increase in group size in wet season could be attributed to natal recruitment. The breeding season of the ostriches is during the dry season from July to October (Brown and Britton 1980). The observed considerable decrease in group size during the dry season might be explained by a decrease in bird detectability in relation to incubation. Other authors have observed a similar pattern of decreasing group size during the breeding season (Sauer and Sauer 1966, Bertram 1992). The decrease in group size during dry season could as well be influenced by food availability and hence dispersion of birds. Spatial and temporal heterogeneity in abundance and quality of food and mineral supplies have been considered as driving forces in various types of migration (Fryxell and Sinclair 1988). Species undertake long-distance movements in response to water and food availability (Crowe 1995).

Most ostrich groups were observed in open habitat types, their preferred habitat. The absence of significant difference in group sizes between the open and closed habitat types suggests that group size is not changed in response to feeding opportunity or predation risk.

Single males were observed more frequently during the dry season, compared to during the wet season. This could be accredited to the breading season being in the dry season where males become territorial. In relation to group composition, the results obtained are similar to Bertram’s (1992), i.e. males commonly occurred singly, and the common group composition was one male and one female. Large groups were mainly composed of a large number of females, leading to the increased skewed sex ratio (female/female+male) with group size.

CONCLUSION

Adult sex ratios are difficult to estimate in an unbiased way due to differences between sexes in their behaviour and ecology (Vanderkist et al. 1999) and the ratios may vary seasonally, spatially or between age groups (Daan et al. 1996). However, skewed adult sex ratios have been found in wild bird populations and are probably due to differential mortality between the sexes as suggested by Donald (2007). Sex ratio has been found to be a tool in conservation efforts as it may provide a useful metric of habitat suitability (Butler and Merton 1992, Zanette 2001). Use of adult sex ratio can be important in assessing the quality of the habitats as a result of increased human pressure in the protected area. Although the results suggest absence of human influence on group size, detailed studies are recommended in a long run on the demography of birds in the partially protected areas. Therefore much more remains to be discovered about the effects of human influence on adult sex ratio.

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FIGURE LEGENDS

Fig. 1. Map showing the Serengeti National Park and Grumeti and Ikorongo Game reserves and Ikoma Open Area.

Fig. 2. Group composition of adult ostriches in the Serengeti National Park (SNP) and partial protected area i.e. Game Reserves and Open Areas (GR/OA).

Fig. 3. Mean (and SE) number of males and females as a function of group size (total number of birds in a group) in ostriches.

Fig. 1.

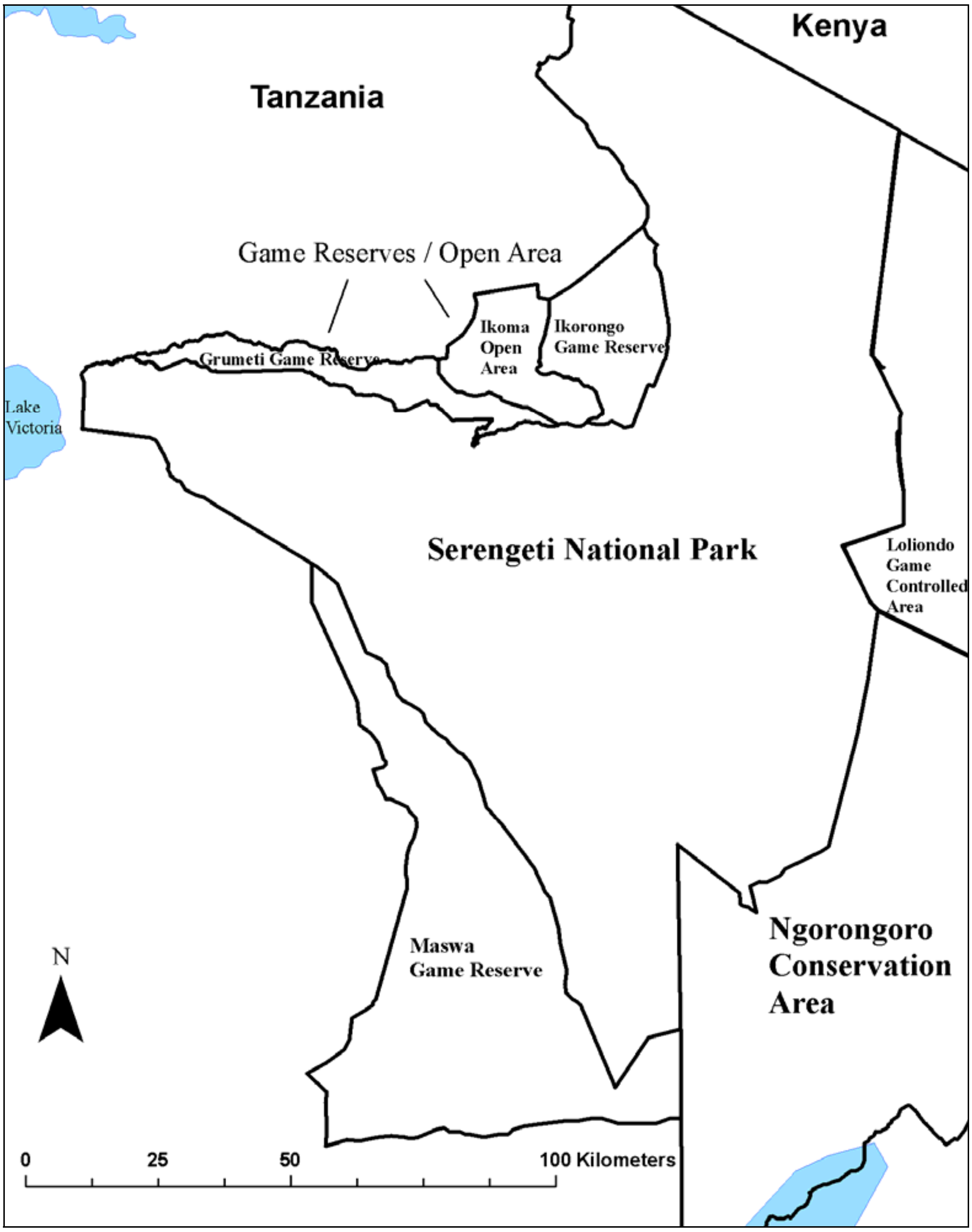

Kenya
Tanzania
Game Reserves / Open Area
Ikoma Open Area
Ikorongo Game Reserve
Grumeti Game Reserve
Lake Victoria
Serengeti National Park
Loliondo Game Controlled Area
Maswa Game Reserve
Ngorongoro Conservation Area
N
0
25
50
100 Kilometers

Fig. 2.

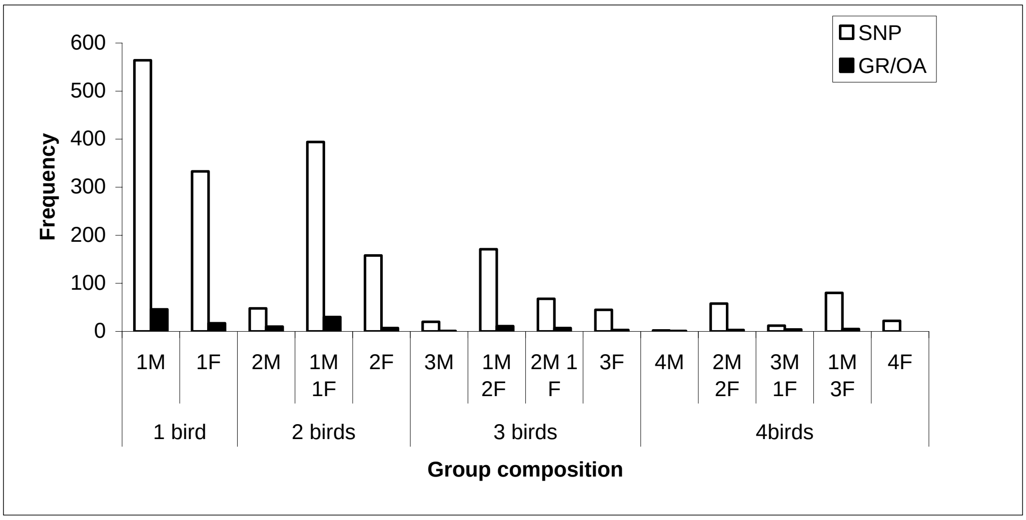
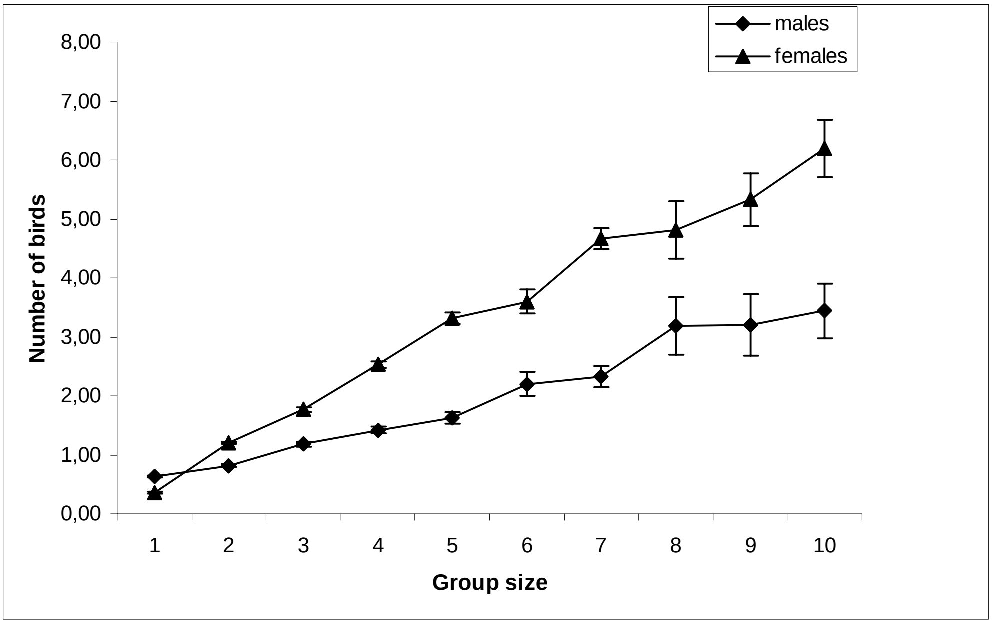

SNP
GR/OA
Frequency
600
500
400
300
200
100
0
1M
1F
2M
1M 1F
2F
3M
1M 2F
2M 1 F
3F
4M
2M 2F
3M 1F
1M 3F
4F
1 bird
2 birds
3 birds
4birds
Group composition

Fig. 3.


males
females
8,00
7,00
6,00
5,00
4,00
3,00
2,00
1,00
0,00
Number of birds
1
2
3
4
5
6
7
8
9
10
Group size

PAPER V

Does illegal hunting affect density and behaviour of African grassland birds? A case study on ostrich

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Abstract

Widespread bushmeat hunting represents one of the major threats towards many mammals and birds in Africa. We studied the influence of illegal bushmeat hunting on large grassland birds, ostrich (*Struthio camelus*) in particular, in Serengeti National Park (SNP) and partially protected areas outside the SNP. First, we documented illegal hunting of birds by using a questionnaire, where we interviewed 115 persons in 6 different villages on the Western and Eastern side of the SNP. Secondly, we studied the effect of illegal hunting on density by driving 4659 km of transects inside SNP and on the adjacent partially protected areas, where the data were analyzed by DISTANCE sampling technique. Lastly, we used flight initiation distance (FID, i.e. the distance between an approaching predator (human) and prey when flight is started), to assess possible impacts on flight behavior from illegal hunting. We found that people from the western side of the SNP, hunted birds extensively, and so was the case for the Maasai people living in the east. However, for the large grassland birds, the Maasai mainly collected ostrich feathers and eggs, whereas the people on the western side utilized all the large bird species investigated. Surprisingly, we found no significant differences in densities between the SNP and the partially protected areas. But ostriches had longer FID to an approaching human in the partially protected areas compared to SNP. Currently illegal hunting does not affect the ostrich population inside the protected areas, but more detailed monitoring of adverse impact is needed for areas close to human settlements.

Keywords Density · Flight initiation distance · Illegal hunting · Ostrich · Serengeti

Introduction

The human population in Africa is rapidly growing and the pressure for resources is increasing both inside and outside protected areas. Although protected areas are recognised as a key element in conservation, studies show that partially protected areas (IUCN category ≤ IV) do not perform as well as strict protected areas (Caro et al. 1998; Caro 1999; Pelkey et al. 2000; Setsaas et al. 2007). Nevertheless, partially protected areas compose a significant part of the protected area network in Southern Africa (WRI 2005). The lack of adequate law enforcement within these areas that can control and regulate human activity (i.e. livestock grazing, illegal bushmeat hunting, firewood extraction) is suggested as an important factor in the observed decline both in mammal populations and vegetation cover (Caro 2000; Pelkey et al. 2000).

Human activity also affect bird populations through hunting, or may indirectly have implications for bird survival and reproduction through changes in their habitat (e.g. overgrazing, deforestation and fragmentation) (Fjeldsa 1999; Lawes et al. 2006; Gottschalk et al. 2007; Manu et al. 2007) or through forcing birds to use sub-optimal areas because of disturbance effects (Rodger and Smith 1997; Herremanns 1998; Blumstein 2006). For instance, Sinclair et al. (2002) found that non-protected areas under cultivation support much fewer bird species compared to the native vegetation inside a strict protected area. Overgrazing by livestock has also negative consequences for some grassland bird species (Herremanns 1998; Thiollay 2006a). Similarly, Thiollay (2006a) documented dramatic declines in large birds in non-protected areas in Burkina Faso, but also noted a decline in bird populations within protected areas close to human settlements. Illegal hunting was suggested to be the main factor, where hunters increasingly targeted large game birds, such as Guinea fowls and Bustards, as other mammalian prey disappeared. This situation appears to be symptomatic for large birds in the rest of North and West Africa, where for example, the ostrich (*Struthio camelus*) which was once widespread is now extinct west of Chad (Thiollay 2006b), northern side of the Sahara (Bertram 1992) and are threatened with extirpation in the western Sahara (Bertram 1992; Ostrowski et al. 2001). Grassland bird species appear to be under less pressure in Southern Africa but there are few studies that have examined possible effects of human activities on bird populations within protected areas in this region (but see Verlinden and Masogo 1997; Herremanns 1998).

The use of behaviour has been proposed as an indicator for assessing disturbance effects of human activity (Caro 1998). Flight initiation distance (FID, i.e. the distance between an approaching predator/human and prey when flight commences) is the most commonly used parameter to assess the effect of human disturbance (reviewed in Stankowitch and Blumstein 2005), and has also been used to investigate the influence of hunting (de Boer et al. 2004; Matson et al. 2005; Setsaas et al. 2007; Thiel et al. 2007). Modeling shows large reductions in the number of food items captured following disturbance, which indicates that a change in shyness might be of conservation significance (Blumstein et al. 2005).

The Serengeti National Park (SNP) in northern-Tanzania is surrounded by several partially protected areas, which have experienced high levels of illegal bushmeat hunting (Dublin et al. 1990; Campbell and Hofer 1995). Illegal bushmeat hunting mainly originates from the villages in the west of the SNP, since the pastoralist Maasai living to the east mainly live on livestock and do not traditionally eat wild animal meat (Campbell and Hofer 1995). The main motivation behind hunting is to increase food supply and cash income (Loibooki et al. 2002; Kaltenborn et al. 2005). Illegal bushmeat hunting is primarily done with snares and targets large herbivores, but if birds also are hunted and eaten by the people living around the Serengeti remains largely unexplored.

The objective of this study was to established the extent to which local people around the SNP utilise three typical large grassland birds, ostriches, kori bustard (*Ardeotis kori*) and guinea fowl (*Numida meleagris*), by comparing tribes with long hunting traditions (e.g. Ikoma and Kurya) on the western side of the national park with the largely pastoral Masaai living on the eastern side. Furthermore, we examined in more detail how successful the partial protected areas were in conserving ostrich populations, in terms of densities and flight behaviour as compared to a strict protected area (SNP).

Methods

Study area

The study was conducted in the Serengeti National Park (SNP) (14,763 km^2) and adjacent partially protected areas: Grumeti (416 km^2) and Ikorongo (563 km^2) Game

Reserves, and Ikoma Open Area (600 km^2), in northern Tanzania (Fig. 1). No human settlement or activities are allowed in the SNP. However, the neighbouring partial protected areas (Ikorongo Game Reserve, Grumeti Game Reserve and Ikoma Open Area) allow trophy hunting whereas the Ikoma Open area allows human settlement and limited human activities such as livestock keeping, legal resident hunting, farming and firewood collection. The area is composed of highland savannah with mainly thorn woodland trees (with species of *Acacia, Comiphora, Ficus, Combretum* and *Podocarpus*) and extensive grass plains (Herlocker 1976).

The Ngorongoro Conservation Area (NCA) is a conservation area stretching across approximately 8,300 km^2. The area is part of the Serengeti ecosystem, and to the north-west it adjoins the SNP and is contiguous with the southern Serengeti plains. The land in the conservation area is multi-use, it is unique as the only conservation area providing protection status for wildlife whilst allowing Masai pastoralist to reside within the protected area. The Masaai live principally on livestock, but cultivation has increased, where the human population within the NCA was 60 000 in 2002 and is increasing with a rate of 3.5% per annum (Boone et al. 2006)

Study species

We specifically focused on three easily identifiable and characteristic grassland bird species: Ostrich (~145 kg), kori bustard (~13 kg males, ~8 kg females) and guinea fowl (~1.3 kg). These three species are ground nesters, which are found in a variety of open habitat types in the Serengeti ecosystem. Ostriches and guinea fowl are found throughout the ecosystem, whereas kori bustards are mostly found on the grasslands and lightly wooded savannas (Stevenson and Fanshawe 2002). Both kori bustard and guinea fowl can fly, whereas ostriches are flightless and rely on running to escape predators.

Data collection

Questionnaire data

Data on illegal bushmeat hunting of birds was collected through questionnaires in six selected villages located in western and eastern SNP from June to July 2006. Our survey encompassed a total of 115 questionnaires, that were systematically selected (every tenth household) from household lists in each village. The villages included Robanda, Natta Mbiso and Nyamakendo on the western side of the Serengeti National Park, where the respondents came from the tribes: Ikoma, Natta and Kurya respectively. On the eastern side of SNP the villages included: Olbalbal, Endulen and Nainokanoka (all located in the NCA) (Fig. 1) and all respondents here where Maasai. The questionnaires focused on: i) methods of hunting, ii) number of birds hunted per week, iii) the bird preferred, and iv) uses of bird products focusing on guinea fowl, kori bustard and ostrich. The hunting of small birds was mainly a juvenile activity, therefore respondents (household head or oldest grown-up) was asked to estimate the number of birds killed, as well as the species.

Transects

Data were collected from April 2004 to October 2005 (19 months), where we used the line transect based distance sampling method (Buckland et al. 2001) to estimate ostrich density (individuals/km^2). The method is based on records of the distance from the line to each object detected when the observer travels along the line (we scanned up to a 1000 m). The occurrence of animals was observed by two observers covering a sector of 180 degrees to the right and left sides of the transect, respectively. Ostriches were detected from a vehicle (Land rover) travelling at 15-20 km per hour. Upon detection a rangefinder (i.e. Leica Geovid 7x42 BDA) was used to determine distance and angle to the transect. The perpendicular distance to the transect were calculated by applying the following recorded measurements: 1) measurements of the distance from the observer to single ostriches or to the centre of clusters and 2) corresponding measurements of the angles between the transect line and the lines between the observer and detected objects. This information was used with the Distance software (Buckland et al. 2001) to fit detection functions that determine the density per main transect (see below). One great advantage of this approach is that we need draw no distinction, within reasonable limits, between habitats with good or poor visibility. The fitted detection function reflects both the decrease in detectability with distance and the lower proportion of animals that are potentially detectable (Buckland et al. 2001). For each sighting, we recorded the number of birds and habitat type (according to Kikula 1980 and Caro 1999), but because of small sample size we pooled habitats types into two categories; closed habitat (woodlands and bushlands) and open habitat (grasslands, wooded grasslands, bushed grasslands and cultivated lands).

The transects were systematically spaced and superimposed on the existing road-system in the study area (Fig. 1). This was necessary due to the ruggedness of the terrain and because cutting new tracks was not allowed. Each transect had a total length of 1 km and transects were spaced with intervals of 2 km. A total of 195 transects were recorded, and sampling was conducted once a month and altogether 4659 km of transects were driven. The areas we estimated density for are the National Park and the adjacent partially protected areas, where the transects within Ngorongoro Conservation Area are pooled together with those on the western side game reserves (Ikorongo and Grumeti)/Open Area (GR/OA). (Fig. 1). The seasons were categorised as wet (November-May) and dry (June-October) seasons. In order to control for possible habitat differences between the areas of comparison, we used ArcView 9.0 to calculate the area (km^2) of vegetation types within a 1 km envelope on both sides of each transect by using a land cover – land use map of the area. The results were recorded according to four categories: grasslands, bushland, woodland and urban/cultivation.

Anti-predator behaviour

Flight behaviour was recorded from August-December 2003, and January-February 2006 along roads and tracks inside and outside the Serengeti National Park between 6:00 am up to 6:00 pm. Only birds engaged in relaxed behaviours such as feeding, resting or preening were examined. Highly vigilant and nesting individuals were not approached. Individuals that were less than 100 m apart were considered one group. Immediately after spotting an ostrich or group of ostriches, we stopped the vehicle and recorded group size, group composition, behaviour, habitat, alertness (individuals being alert or not before the approach) and the distance from the car to the centre individual (i.e. starting distance). Then the testperson (wearing neutral coloured cloths) approached the ostrich(es) at a steady pace (approx. 0.5 m/s). When the birds fled the testperson immediately stopped and the distance to the testperson was recorded. The FID was the difference between the starting distance and the distance to the testperson when the bird(s) took flight. We sampled ostriches over a large area, but in order to minimise the potential problem of pseudoreplication we never re-sampled an area before at least a week had passed. However, according to Runyan and Blumstein (2004) a modest degree of pseudoreplication does not affect results in FID studies.

Statistical analyses

We used DISTANCE 5.0, release 2 (Thomas et al. 2006) to estimate densities (ostriches/km^2). Right truncations of sighting distance frequency distribution were performed by visual inspection and by applying the distance corresponding to a recommended truncation value of 0.15 of the detection function (Buckland et al. 2001). The detection function reflects both the decrease in detectability with distance and the lower proportion of animals that are potentially detectable (Buckland et al. 2001). The DISTANCE software estimates the detection probability of an animal as a function of distance. The negative exponential, global detection function with cosine expansions (Buckland et al. 2001) was chosen using Akaike's Information Criterion (AIC) corrected for small samples and chi-square goodness-of-fit tests (Sakamoto et al. 1986). We calculated ostrich densities for areas and habitat types having more than 40 observations although a sample size of minimum of 60 observations is recommended by Buckland et al. (2001). Up to twelve models were generated in each analysis, and the best model was selected basing on the lowest ΔAIC_c. The densities were considered statistically significant if the confidence interval values did not overlap (Buckland et al. 2001).

Predators do not commence approaches of prey at fixed distances, and it is not surprising that starting distance strongly influences alert distance and FID, as previous studies have shown in birds (Fernández-Juricic and Schröder 2003; Blumstein 2003). Thus, we incorporated starting distance as an independent variable in all our tests. We used linear-mixed models, to account for possible year effects due to sampling over 2 different years (the two testperson used was also nested inside the same variable), in order to explore the variables influencing FID, with year set as a random effect (see Crawley 2002). The predictor variables included in the models were therefore: starting distance, area (inside or outside the national park), alertness (whether or not the focal individual was alert prior to the approach), group size and group composition (male, female, mixed). However, the analysis was restricted to approaches done in open vegetation, due to low sample size. In the analysis the variables FID and starting distance were square root transformed to improve normality of residual errors. We selected the most parsimonious model from a set of appropriate models according to Akaike Information Criterion corrected for small samples (AIC_c) (Burnham and Anderson 2002). The best models were those with lowest AIC_c values, highest Akaike weights (ω_i) and $\Delta AIC_c < 2$, however the most parsimonious model was the one with lowest number of parameters among those with $\Delta AIC_c < 2$. The Akaike weight indicates the probability that the model is the best among the whole set of candidate models. The analyses were performed using R 2.3.0 Software (R Development Core Team 2006). Data are presented as mean ± standard error.

Results

Illegal hunting

No one volunteered that anyone in their households or they themselves hunted (small and large birds), but hunting of small birds was primarily done by juveniles (e.g. shepherds). However, the majority of the local people interviewed in both western Serengeti (98.3%, n = 59) and NCA (71.4%, n = 56) admitted that people in their villages hunted small sized birds (< 1kg, Table 1) for food, but it was more usual in the western Serengeti ($\chi^2 = 16.47$, df = 1, $P < 0.001$). The commonly hunted small birds were doves and francolins in western Serengeti and NCA respectively (Table 1). The hunting methods were similar in both areas, where the use of birdlime (adhesive substance made from tree species commonly of genus Cordia, Grewia and Euphobia, used in trapping birds) (48.9 %) was most common, followed by: slingshot (34.7 %), dogs (12.2 %) and other kinds of weapons (i.e. stick and stones, 4.1 %). The respondents estimated how many small birds per week that was hunted on average, where there was no significant difference between the two areas (western Serengeti: 9.8 ± 1.3 small birds, NCA: 8.71 ± 1.7 small birds) (Mann-Whitney U test = 494.5, Z = -0.72, $n_1 = 46$, $n_2 = 24$, P = 0.47).

Hunting of large birds (> 1 Kg) was done by juveniles and adults. A wide variety of weapons were used according to respondents to hunt large grassland birds, where snares were the most common method to catch ostriches (Table 2). The hunting tribes in western Serengeti replied that all the focal grassland birds were hunted for meat, and they also collected eggs and feathers. On the other hand, the Maasai living in NCA claimed to collect only eggs and feathers from ostriches and guinea fowl (Table 2), and did not use any product of kori bustards (Table 3). Respondents in western Serengeti replied that guinea fowl was the most preferred species (83%), whereas since the respondents in NCA did not hunt large grassland birds, they answered that ostrich eggs were most preferred (91%).

Nobody replied that they themselves had traded bird products, but overall 33.9% of the respondents replied that people in their village had sold ostrich products, such as eggs (price per egg: US$ 1.03±0.9, n = 23) and meat (1-2 kg dry meat: US$ 1.4±1.0, n = 10), and that some of the buyers were villagers (27.8%), tourists (2.6%) and hotels (2.6%) (no distinction was made between local and tourist hotels). Only respondents from western Serengeti replied that people in their village sold products from guinea fowl, where 20.9% said that the villagers sold eggs (price per egg: US$ 0.14±0.1, n = 13) or meat (whole bird: US$ 1.47±0.9, n = 11). Here 20% claimed that products had been sold to fellow villagers, while only one replied that products had been sold to tourist (0.9%).

Density estimates

A total of 634 ostriches were recorded for which density estimates were obtained. The overall density (i.e. national park, NCA, game reserves and open areas combined) was (0.16 ± 0.03 ostriches/km^2) (Table 4). There were no statistical differences in ostrich density between the national park and the partially protected areas, between wet and the dry season or in the open habitats as compared to closed habitats. But there was a significant difference in the percentage area of each of the 4 vegetation types along the transect envelopes inside and outside the Serengeti National Park ($\chi^2 = 760.6$, df = 3, $P < 0.001$).

Anti-predator behaviour

We conducted a total of 129 approaches toward ostriches. There were three models of a total of 16 candidate models considered that had a Δ AIC$_c$<2 in the analysis on FID (Table 5). However, the first model contained three variables and was therefore not the most parsimonious. The most parsimonious model (second model) included the variables starting distance and area. Starting distance increased with FID, and FID was larger in the partially protected areas (Table 5, 6, Fig. 2).

Discussion

Illegal bushmeat hunting

Bushmeat is an important part of the diet in most areas in Sub-Saharan Africa (Anstey 1991; Barnett 2000). The use of birds in the Serengeti ecosystem also reflects this, where the majority of the respondents replied that people in the village (both juveniles and adults) hunted birds. However, there is a slight distinction between the different tribes in regards to consumption of birds. The traditional hunting tribes in the western Serengeti, such as Ikoma, Natta and Kurya hunt and collect eggs from most birds. Of the large grassland birds, the kori bustard was the least preferred bird (see Table 3), whereas almost every product from the ostrich and guinea fowl was put into use. However, for the Maasai residing within the NCA, our results indicate that it is mostly the young shepherders that hunt smaller birds. The large grassland species are mostly ignored, except Ostrich eggs that are commonly collected by the Maasai. Ostrich eggs have long being prized and people have found them an invaluable food source and apply empty shells as practical water vessels or ornaments (Bertram 1992, Giazi et al. 2006). In addition, respondents claimed to use eggs in treatment of diseases such as asthma and tuberculosis, and use egg shells as ornaments during traditional dances and circumcision ceremonies. A worrying result is that Ostrich eggs, have become a commercial product, where some of the respondents claim that they are collected for sale, both to local villagers but also to tourists. Enforcing wildlife laws within these protected areas is therefore vital. Moreover, encouraging visiting tourist more explicitly to abide with wildlife regulations on the trade in wildlife products should be emphasised upon arrival at the entrance to protected areas. It may also be necessary to consider the possible inclusion of bird species, through ecotourism based operations and/or sustainable utilisation, as part of community-based conservation schemes in order to involve local people as stakeholders and to create incentives for conserving their avifauna.

Density

The density of ostriches within the partially protected areas was not significantly different from the density within the SNP. However, the areas outside the SNP differed in respect to vegetation types, where they contained more woodlands than the grassland dominated National Park. This may have contributed to the observed densities. Other studies on mammals in the Serengeti ecosystem have found lower densities in the areas outside the National Park and linked this to the widespread illegal bushmeat hunting conducted in the area (Dublin et al. 1990; Campbell and Borner 1995; Hofer et al. 1996; Rusch et al. 2005; Setsaas et al. 2007). In West Africa, Thiollay (2006a) reported that the decline of mammals caused illegal hunters to increasingly target large grassland birds. However, the Serengeti ecosystem still sustains large concentrations of herbivores, which may indicate that currently illegal hunters only kill large bird species opportunistically. Livestock grazing which occurs within the partially protected areas (legally within NCA and occasionally illegally inside the Grumeti and Ikorongo Game Reserves) may also cause changes to the habitat of birds and may damage the reproductive success of ground nesters through trampling and disturbance (Rodger and Smith 1997; Herremanns 1998; Lord et al. 2001). However, location of the transects may not have captured the full extent of possible effects of human activities, since they were mostly placed within the protected areas and relatively far from areas with high human density. Sinclair et al. (2002) noted that the abundance of species found in cultivated areas in relatively high human density areas in north-western Serengeti, was only 28% off that for the same species in native savannah. This was mostly due to removal of trees and a decrease in grass-layer insect abundance and diversity. Also Thiollay (2006a) noted declines in bird diversity and abundance in high human density areas and that the disappearance of game birds also contributed to a dramatic decline in raptor species (Thiollay 2006c). Both the human population in NCA and in the western Serengeti are growing rapidly, which means that human impact is likely to increase in the future (Campbell and Hofer 1995; Boone et al. 2006). Considering the extensive use of birds it is therefore crucial that monitoring programs are expanded to also include the avifauna. This may serve to guide protected area managers to make more informed decisions about how to manage the location and size of human settlements within the NCA, as well as the level and type of human activity permitted (both NCA and Game Reserves) in order to ensure that biological values do not deteriorate.

Flight behaviour

The most parsimonious model indicated that two variables, starting distance and area, have a great influence on FID. This underlines that risk is assessed dynamically and that also ostriches flee at a greater distance as starting distance increases (Ydenberg and Dill 1986; Blumstein 2003). This response is probably stronger in large birds that rely solely on running to escape possible predators than in species that can fly, which might make them particularly vulnerable to disturbance (Gaston and Blackburn 1995; Fernández-Juricic et al. 2006; Blumstein 2006). Area also affected FID, but since illegal hunters do not currently specifically target ostriches and since the prevailing hunting method of illegal bushmeat hunters is snaring, it appears that ostriches might instead be negatively affected by the unregulated legal hunting. The partially protected areas in the west is subject to legal hunting from a number of government institutions (Holmern et al. 2004), where hunting of large herbivores is mostly conducted from vehicles. In some instances drivers give chase to animals over long distances thus causing great distress to other wildlife species (Holmern, pers.obs. 2003), this may also cause ostriches also to become more flighty.

Conclusion

Our results suggest that illegal hunting currently does not affect ostriches adversely in the Serengeti ecosystem. However observed changes in flight behaviour in the partially protected areas may have indirect fitness cost to the populations. On the other hand, the documented extensive hunting of small birds, and collecting and trade of eggs highlight that protected area managers need to develop clear strategies and policies for the location of human settlements, regulations for extraction of resources and also to develop policies that regulate human population size within protected areas. In order to address possible consequences of human disturbance on the avifauna in the Serengeti ecosystem we recommend that a monitoring program for birds is established within protected areas.

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Tables:

Table 1 Percentage frequency of small birds hunted in western Serengeti and Ngorongoro Conservation Area (NCA)

Western Serengeti	Percentage	NCA	Percentage
None	23.7	None	87.5
Doves	47.5	Francolin	7.1
Francolin	20.4	Parrot	3.6
Parrot	5.1	Weaver*	1.8
Weaver*	11.9		
Total	108.6		100

*Weaver- all small colourful birds were regarded as weavers by the respondents

Table 2 Weapons used by illegal hunters to hunt the focal large grassland birds (Ser = western Serengeti, Ngorongoro Conservation Area = NCA)

	Ostrich		Guinea fowl		Kori bustard	
Weapon	**Ser (%)**	**NCA (%)**	**Ser (%)**	**NCA (%)**	**Ser (%)**	**NCA (%)**
None	11.7	1.8	6.8	96.4	98.3	100
Snare	47.5	-	-	-	-	-
Collection of eggs & feathers	13.6	98.2	10.2	3.6	-	-
Spear	11.9	-	-	-	-	-
Rope	8.5	-	67.8	-	-	-
Bow & arrow	3.4	-	-	-	1.7	-
Gun	3.4	-	-	-	-	-
Dogs	-	-	10.2	-	-	-
Birdlime	-	-	6.8	-	-	-
Slingshot	-	-	1.7	-	-	-

Table 3 Use of bird products as recorded in the villages.

Product	**Ostrich (%)**		**Guinea Fowl (%)**		**Kori bustard (%)**	
	Serengeti	Ngorongoro	Serengeti	Ngorongoro	Serengeti	Ngorongoro
None	11.9	1.8	1.7	96.4	89.8	100
Eggs	76.3	94.7	89.9	1.8	-	-
Feathers	57.7	96.5	11.9	1.8	1.7	-
Meat	55.9	-	89.9	-	8.5	-
Total	201.8	193	193.4	100	100	100

Table 4 Total number of observations (with total number of ostriches in parentheses) and densities according to area (inside and outside SNP), season and habitat categories. Densities (per km^2) are reported as mean ± SE (95% confidence interval in parenthesis).

	Description	**N**	**Density ± SE (95% CI)**	**Goodness of fit (P value)**
Overall density		207 (634)	0.16 ± 0.03 (0.11-0.22)	0.90
Area	Outside SNP	52 (137)	0.25 ± 0.09 (0.12-0.52)	0.78
	Inside SNP	155 (497)	0.15 ± 0.03 (0.10-0.21)	0.94
Season	Wet	115 (422)	0.29 ± 0.06 (0.20-0.44)	0.95
	Dry	92 (212)	0.17 ± 0.04 (0.11-0.26)	0.77
Habitat	Open	144 (450)	0.22 ± 0.04 (0.07-0.26)	0.67
	Closed	63 (184)	0.13 ± 0.05 (0.15-0.32)	0.94

Table 5 The five best candidate models and the global model explaining flight initiation distance (FID) for ostriches in the Serengeti ecosystem. The models are ranked by the Akaike Information Criterion corrected for small samples (AIC_c). (K = number of parameters; ΔAIC_c = difference in AIC_c between the best model and the actual model; ω_i = Akaike weights). The most parsimonious model is on the top of the list. Analyses are based on 129 human approaches (STD = starting distance).

Model	**K**	**AIC_c**	**ΔAIC_c**	**ω_i**
STD + alert + area	6	437.1	0.000	0.252
STD + area	5	438.1	1.035	0.150
STD + alert	4	438.2	1.115	0.144
STD + alert + area + group size	7	439.3	2.192	0.084
STD + alert + area + group composition	8	439.5	2.363	0.077
Global model: STD + alert + area + group size + group composition	9	441.7	4.641	0.025

Table 6 Estimate for the most parsimonious model of flight initiation distance (FID) for ostriches in the Serengeti ecosystem, Tanzania. STD = starting distance. For more details see Table 5.

Coefficients	**Estimate**	**SE**	***T***	***P*-value**
Intercept	-0.63	0.54	-1.16	0.248
Starting distance	0.95	0.03	30.05	<0.001
Area	0.78	0.38	2.05	0.043

Figure legends:

Fig. 1 Map over the protected areas in the Serengeti ecosystem. Thick lines denote the protected areas. The western Serengeti shows all villages as grey pentagons and the study villages used for the questionnaire survey as black pentagons. In the Ngorongoro Conservation Area only the three study villages are shown as black pentagons. In addition, the positions of transects are shown as short grey lines, whereas circles show the locations of FID experiments.

Fig. 2 The effect of the animals displaying alert behaviour prior to the approach and the effect of area on flight initiation distance (FID), in the Serengeti ecosystem, Tanzania. The thick line represents the 1:1 relationship between the starting distance and FID. Figure shows the effect of area on FID (inside the National Park: dotted line, □ and outside the National Park: dashed line, ■).

Figures:

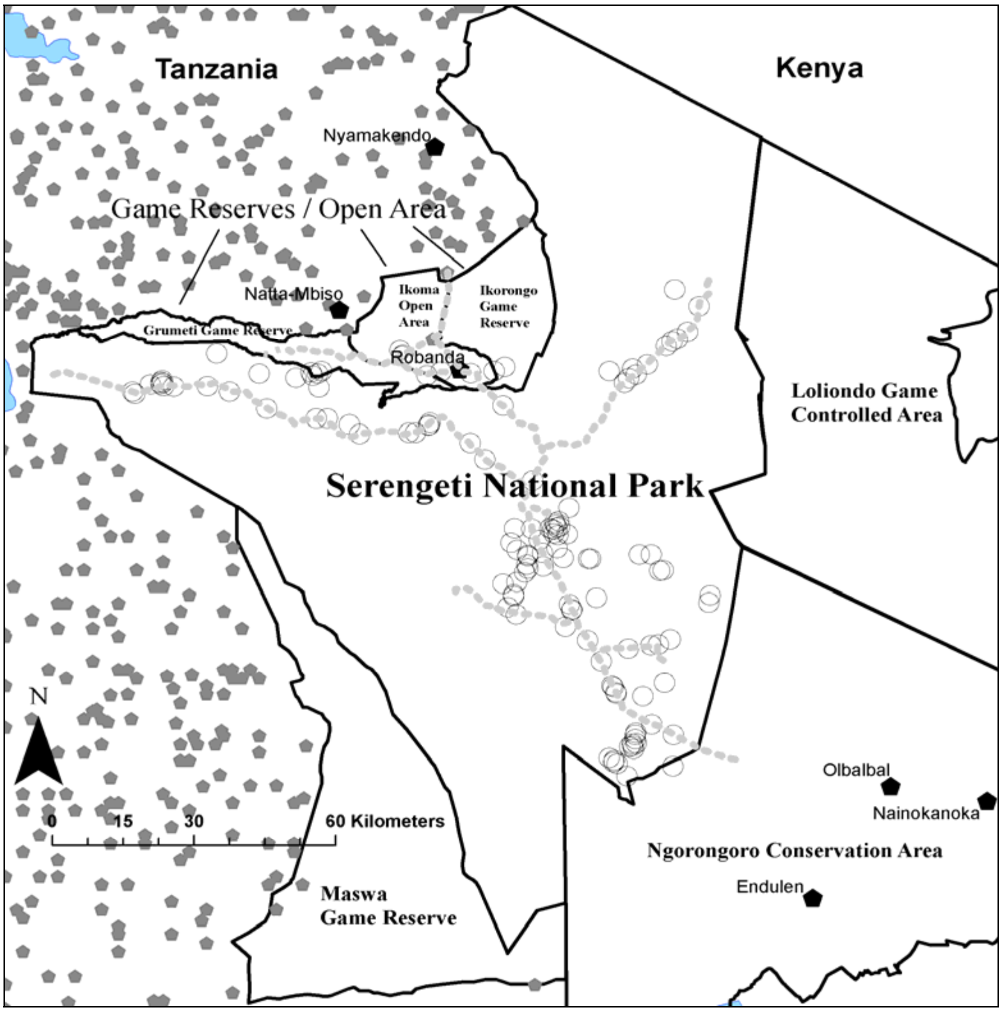

Fig. 1

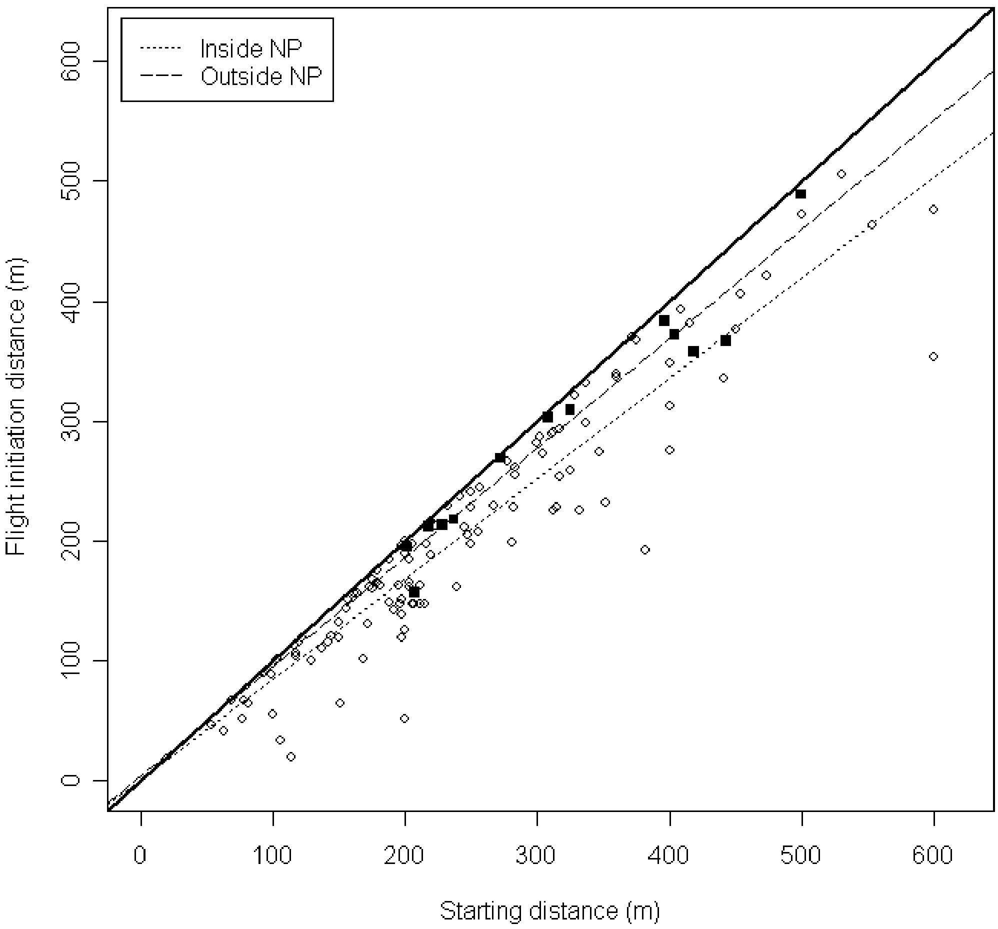
Inside NP
Outside NP
Flight initiation distance (m)
Starting distance (m)
0
100
200
300
400
500
600
0
100
200
300
400
500
600

Fig. 2

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*

1987 Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988 Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988 Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988 Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988 Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989 John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989 Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989 Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989 Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990 Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990 Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990 Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990 Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990 Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990 Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991 Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991 Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991 Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991 Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991 Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991 Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991 Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991 Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.

1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992 Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992 Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992 Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994 Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.

1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.

1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.

1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development

2002 Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002 Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003 Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003 Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003 Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003 Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003 Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003 Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003 Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003 David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003 Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003 Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004 Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004 Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004 Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004 Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004 Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004 Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming

2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	Phd Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	phD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania

2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	phD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape