Investigating the possible change in breeding strategy of African Black Oystercatchers

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Abstract

Avian clutch size varies considerably among species. Clutch size ranges between the typically larger plastic clutches produced by indeterminate layers, and the fixed modal clutch sizes of determinate layers. The small clutch sizes of determinate laying waders are not well understood with most theories focussed around rearing costs, predation, and prey limitations. However this does not explain the short term changes (decadal) which may occur within wader species, such as the change in clutch size of the Eurasian Oystercatcher (*Haematopus ostralegus*) whereby larger than modal clutches were produced through a change in mating habits resulting in polygamy and egg dumping.

African Black Oystercatchers (*Haematopus moquini*) have a modal clutch size of two eggs but occasionally lay one or three eggs. It has been noted that an increase in frequency of larger three- and even four-egg clutches has occurred over the last few decades. By analysing extensive historical nest records dating back five decades I verified the occurrence of this increase in three-egg clutches over many of the sites within their breeding range. As African Black Oystercatchers are very territorial, co-operative polygyny was rejected as a sole cause (through observations). As eggs were found to be significantly similar (through intra-clutch egg shape comparisons) within clutches egg-dumping as a cause was also rejected. It was thus established that the increase in three-egg clutch frequency was indicating an increase in breeding effort. On further analysis of this increase, it was discovered that three-egg clutches offer no benefit to species fitness or breeding success as they do not result in an increased fledgling output to those of the smaller two-egg clutches. This is primarily due to inefficient incubation as a result of the extra egg, and the inability to maintain and feed a larger brood size.

This study validates previous assertions that three-egg clutch frequency is increasing for African Black Oystercatchers. This increase is a substantial change in life history. In understanding what the primary influencing factors are, the information can further aid in the understanding of all wader clutch sizes. The methods adopted within this study can also be used to establish if clutch size increase is occurring within other species and test for factors such as polygyny and egg dumping. These changes in breeding strategy are uncommon, and if they occur it is important to understand if the increase is beneficial for the species. African Black Oystercatchers exhibiting this increase do not produce more fledglings or improve their breeding success compared with individuals laying two-egg clutches. With experience they may be able to brood three-egg clutches effectively and improve population growth. It is thus important to continue observing this species.

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Plagiarism declaration

I know the meaning of plagiarism and declare all the work in the dissertation, save for which is properly acknowledged, is my own.

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General introduction – Intraspecific variation in clutch size in waders: implications for African Black Oystercatcher conservation

Clutch size (number of eggs per female per nest) varies considerably among bird species. While some groups (e.g. Procellariiformes) invest in only one egg per clutch, others may lay larger numbers, with records of up to 22 eggs in a single nest (Jetz et al. 2008). Clutch size is one means of regulating the population (Ashmole 1963), and a species' optimal clutch size is selected based on adult and juvenile mortality (Brockelman 1975). As a larger clutch produces more young in optimal conditions it can be favoured, but in poorer conditions brood competition occurs and the cost of producing a large clutch may impact the female's health, affecting her ability to relay (Hanssen et al. 2005) or survive until the next breeding season (Steven 1980).

Several theories attempt to explain intraspecific clutch size variation. Most location-based theories including increases in latitude (Moreau 1944a, Lack 1947, Dunn et al. 2000, Jetz et al. 2008) and longitude (Murray 1976), explain clutch size variation in terms of a site-specific genetic or phenotypic response driven by resource availability, or seasonal variability (Moreau 1944a, Lack 1947). Other explanations focus on mating and nesting habits (polygamy and egg dumping; (Heg and Treuren 1998)) or physiological factors such as bird mass and age (Moreau 1944a, Haywood and Perrins 1992). Birds can be categorized as either indeterminate or determinate layers defined by their response to the removal or addition of eggs to their nest during laying (Kennedy, 1991). For indeterminate layers such as the Anseriformes, clutch size is fairly plastic as an extra egg is easily added to a clutch when resources allow. For determinate layers such as the European (Kennedy, 1991) or New Zealand Oystercatchers (Baker, 1969) however, this is not common and may imply a change in life history. Many threatened bird species are determinate layers (e.g. sea birds, waders and many raptors) and it is important to understand what can cause this change and potentially increase the breeding output of birds like the African Black Oystercatcher (*Haematopus moquini*). In this thesis I attempt to determine the factors influencing clutch size and the impact clutch size has on breeding success by analysing the recent increase in frequency of three-egg clutches in the African Black Oystercatcher.

What causes clutch size variation?

Waders such as oystercatchers belong to the suborder Charadrii (Table 1.1) which may have originated from an ancestor which laid four-egg clutches (MacLean 1972, del Hoyo et al. 2006). It is not well understood what causal factors influence intra-specific clutch size variation within this suborder, but resource availability (Loewenthal 2007), geographic (Väisänen 1977, Nol et al. 1984) and seasonal variation (Rowe et al. 1994, Krapu et al. 2002), predation risk (Summers and Hockey 1980), female physiological factors (Nol et al. 1997) and breeding strategy (polygyny and egg dumping) (Heg and Treuren 1998, Totterman and Harrison 2007, Craik 2010) have been focal points in existing research. Being determinate layers, waders' clutch size is genetically determined which makes short term response to environmental change unlikely.

Resource availability

The availability of food resources during both breeding and non-breeding seasons has been found to play an important role in determining the clutch size of waders. Spikes in food abundance may result in an increase in clutch size in determinate layers such as the Tengmalm's Owl (*Aegolius funereus*) (Hörnfeldt and Eklund 1990, Korpimäki and Hakkarainen 1991), however the reduction in clutch size when resources are scarce tends to be more common. This arises as the ability to acquire food, particularly in temperate, resource-limited areas has been found to reduce overall clutch size (Skutch 1985, Martin et al. 2000). Food availability also strongly influences the proportion of pairs able to breed within a season (Skutch 1985, Martin et al. 2000). In areas where resources are more abundant, bird density and range size (Figuerola and Green 2006) have a greater effect on clutch size then food availability alone (Skutch 1985, Martin et al. 2000). This may imply that clutch size in high density areas is naturally restricted due to competition for resources, and an increase may occur following a decrease in competition, as a result of an introduction to a new area (Moreau 1944b, Cassey et al. 2005, Congdon 2010), population instability (Cody 1966), or an increase in resources at the site.

Geographic and seasonal variation

This resource driven change in clutch size is the probable cause for the correlations between clutch size and location that exist for indeterminate layers (Moreau 1944a, Lack 1947, Murray 1976, Dunn et al. 2000, Jetz et al. 2008), and a few waders. Latitudinal and longitudinal correlations between clutch size have been recorded in the Red Phalarope (*Phalaropus fulicarius)* (Schamel and Tracy 1987), European Oystercatcher (*H. ostralegus*) (Väisänen 1977), and American Oystercatcher (*H. palliatus*) (Nol et al. 1984), but no such patterns have been found in more range restricted species such as the African Black Oystercatcher (*H. moquini*) and American Black Oystercatcher (*H. bachmani*) (Summers and Cooper 1977, L'Hyver and Miller 1991).

Species occupying larger population ranges may experience variable seasonal factors which may result in geographical variances in clutch size. This is seen in birds that lay larger clutches in areas with warmer winters (Przybylo et al. 2000), and a warmer average temperature during the breeding season (Olsen et al. 2008). The timing of egg laying within the season is important as the success of the first laid clutch is greater than subsequent clutches (Verhulst and Nilsson 2008) which may be the cause for larger initial clutches (Gurney et al. 2011). A reduction in clutch size in waders consequently occurs as the breeding season progresses (Väisänen 1977, Nol et al. 1984, L'Hyver and Miller 1991), as a result of a reduction in female physical condition after each lay (Moreau 1944a, Nol et al. 1984).

Physiological factors

A bird’s age (Moreau 1944a) and health (Verhulst and Nilsson 2008) can influence clutch size. Pairs laying for the first time tend to lay smaller clutches, possibly due to a smaller body size and inexperience, while older birds have been found to lay larger eggs (Thompson and Hale 1991, Nol et al. 1997) but not larger clutches (Lessells et al. 1989, Figuerola and Green 2006). This age difference may relate to female size as larger females often lay the largest clutches (Moreau 1944a) and egg biomass (Thompson and Hale 1991) in waders. A larger adult size may also increase the incubation efficiency of these pairs as incubation limitations result in brood reduction caused by clutch abandonment, reduced hatchability, hatching asynchrony and predation (Arnold 1999, Lengyel et al. 2009).

Predation risk

Wootton (1986) proposed that “spreading the risk” by having many small clutches as opposed to a few larger ones, may be optimal for birds in high predation areas. Thus nest site and territory selection are important determinants of clutch size as birds tend to lay smaller clutches at sites with higher predation risk (Lima 1987, Martin et al. 2000). As clutch size is a heritable trait (Postma and van Noordwijk 2005), resulting in offspring producing near identical clutch sizes to their parents (Perrins and Jones 1974), high predation rate is believed to favour for the evolution of smaller clutch sizes in plovers (Summers and Hockey 1980). Following a season of high predation, Collared Flycatchers (*Ficedula albicollis*) (Doligez and Clobert 2003) and Siberian Jays (*Perisoreus infaustus*) (Eggers et al. 2006) had reduced clutches as a result of clutch size plasticity (Doligez and Clobert 2003, Eggers et al. 2006), although this short term change has not been documented in waders.

Polygyny and egg dumping

Two major factors altering clutch size in waders is egg dumping (when one female lays its eggs in another female’s nest) and polygyny (one male to multiple females). Intra-specific (Payne 1977) and interspecific (Yom-Tov 1980) parasitism of nests is fairly common, the best known case being cuckoos which even use egg mimicry to ensure their eggs are not rejected (Moksnes and Røskaft 1995). Examples of this intraspecific egg dumping also exist for oystercatchers (Craik 2010), although this is usually hard to confirm without genetic testing.

Like egg dumping, polygamous mating may result in eggs from more than one female being laid in a single nest. Although monogamy is the most common mating system in birds, polygamy (polygyny, polyandry and polygynandry) is well documented among waders (Selander 1965, Heg and Treuren 1998) (Table 1.1). Polygyny occurs when a male mates with two or more females, often due to a higher female to male ratio, making it easier for a male to defend more than one female. Polygyny can be either cooperative or aggressive, defined by the females’ ability to fend off other females (Slagsvold and Lifjeld 1994). Within cooperative polygyny the females form a bond and usually lay their eggs within the same nest while an aggressive polygynous group usually has separate nests and may result from a males territory overlapping that of a widowed female (Slagsvold and Lifjeld 1994, Heg and Treuren 1998). Polygyny is known to result in larger than modal clutch sizes (Table 1.1) amongst the European Oystercatcher (*Haematopus ostralegus*) which can produce clutches of up to six eggs (Heg and Treuren 1998), and the Australian Pied Oystercatcher (Haematopus longirostris) which produce a clutch size of up to four eggs (Totterman and Harrison 2007). As there have been records of larger clutch sizes in the African Black Oystercatcher it is believed that cooperative polygyny may be occurring within this species as well.

Clutch size in African Black Oystercatcher

African Black Oystercatchers are endemic to southern Africa, occurring from southern Angola (Simmons et al. 2009) to southern Mozambique (Brown and Hockey 2007). They breed between Lüderitz, Namibia (Hockey 1983) and southern KwaZulu-Natal (nest records), with most breeding pairs found along the west coast (Summers and Cooper 1977) (Figure 1.1). They nest on the shore feeding on mussels and limpets (Hockey 1984, Kohler et al. 2009a), but have also been noted to feed on insects (Ryan and Visagie 2008), polychaetes (Hockey 1984), and potentially even fish (Paijmans 2013). Populations have increased over recent decades which is likely due to stringent protection laws, increased breeding success (Tjørve and Underhill 2006), and increasing food stocks (Loewenthal 2007).

African Black Oystercatchers are monogamous and pairs protect a single nesting territory year round (Hockey 1982a). There is some anecdotal evidence (Phil Whittington and Tony Tree, pers. comm.) of a third adult accompanying a pair of African Black Oystercatchers which may imply polygyny or egg dumping, but this remains unconfirmed. Pairs lay between one and three eggs from November to March (Tjørve and Underhill 2008), with nest frequency peaking in January (Summers and Cooper 1977, Tjørve and Underhill 2008). If the initial clutch is unsuccessful they may relay within the same season (Hockey 1982a). Breeding success is inherently low due to wave action (Calf and Underhill 2005, Jeffery and Scott 2005, Braby and Underhill 2007), wind-driven sand storms (Jeffery and Scott 2005), predation by snakes (Jeffery and Scott 2005), birds (Braby and Underhill 2007), dogs and other mammals (Leseberg et al. 2000, Jeffery and Scott 2005).

With a modal clutch size of two, African Black Oystercatchers have shown some signs of increase in three-egg clutches in recent years (Table 1.2), although most of the more recent records remain unpublished. The first three-egg clutch was recorded in 1924 in Knysna (Carlisle 1929) and they have occurred very rarely since then. Summers and Cooper (1977) only recorded one three-egg clutch, and only a slight increase of three-egg clutches was noted over a long term study of 20 years in De Hoop (Jeffery and Scott 2005). In recent decades however the frequency of three-egg clutches has increased with three four-egg clutches being recorded since 1999 (unpubl. data), where there were none recorded before.

Table 1.1. Mating system and clutch size of the suborder Charadrii and all oystercatcher (*Haematopus*) species (data from del Hoyo et al. 2006)

Family	No. of Genera	Species in genera	English name	Area	Pairing	Clutch Size
Ibidorhynchidae	1	1 species	Ibisbill	Asia	Monogamous	2-4 eggs
Recurvirostridae	3	7 species	Avocets and stilts	World wide	Monogamous	3-4 eggs
Jacanidae	6	8 species	Jacanas	World wide	Polygamous	3-4 eggs
Rostratulidae	2	2 species	Painted snipes	Nearly world wide	Polyandrous and monogamous	2-5 eggs
Dromadidae	1	1 species	Crab plover	Indian Ocean coasts	Monogamous	1-2 eggs
Burhinidae	2	9 species	Thick-knees	World wide	Monogamous	1-3 eggs
Glareolidae	6	17 species	Coursers and pratincoles	Eurasia, Africa and Australia	Monogamous	1-3 eggs
Scolopacidae	26	86 species	Snipes, sandpipers and phalaropes	World wide	Most monogamous	1-6 eggs
Pedionomidae	1	1 species	Plains-wanderer	Australia	Polyandrous	2-5 eggs
Thinocoridae	2	4 species	Seed snipes	South America	Monogamous	4 eggs
Chionidae	1	2 species	Sheathbills	Antarctic	Monogamous	1-4 eggs
Charadriidae	10	67 species	Plovers and lapwings	World wide	Most monogamous	1-4 eggs
Haematopodidae	1	11 species	Oystercatchers	World wide	Most are monogamous although records exist of polygyny in the *H.ostralegus* and *H.longirostris*	1-4 eggs
		H.moquini	African Black Oystercatcher	Africa		1-2 rarely 3 eggs
		H.meadewaldoi	Canary Islands Oystercatcher	North West Africa		1-3 eggs
		H.bachmani	American Black Oystercatcher	North America		1-4 eggs
		H.palliatus	American Oystercatcher	America		1-4 eggs
		H.longirostris	Australian Pied Oystercatcher	Australia		1-3 rarely 4 eggs
		H.ater	Blackish Oystercatcher	South America		1-2 eggs
		H.chathamensis	Chatham Oystercatcher	New Zealand		2-3 eggs
		H.ostralegus longipes	Eurasian Oystercatcher	Eurasia		2-4 eggs
		H.ostralegus osculans	Eurasian Oystercatcher	East Asia		2-4 eggs
		H.ostralegus ostralegus	Eurasian Oystercatcher	Western Europe		2-4 eggs
		H.leucopodus	Magellanic Oystercatcher	South America		1-2 eggs
		H.fuliginosus	Sooty Oystercatcher	Australia		2-4 eggs
		H.finschi	South Island Oystercatcher	New Zealand		2-3 eggs
		H.unicolor	Variable Oystercatcher	New Zealand		2-3 eggs

The increased food resources from the invasive Mediterranean Mussels (*Mytilus galloprovincialis*) is believed to be one of the factors affecting the clutch size of the African Black Oystercatcher (Loewenthal 2007), as they were first noted on the West Coast in 1985 and since then spread into southern Namibia (Hockey and van Erkom Schurink 1992, Branch and Steffani 2004). It was introduced to Port Elizabeth in 1990 (Hockey and van Erkom Schurink 1992), and now comprises a large percentage of the total rocky shore biomass (Hockey and van Erkom Schurink 1992). The invasion by *M. galloprovincialis* has greatly reduced the number of native bivalve and limpet species, including black mussels (*Choromytilus meridionalis*) and ribbed mussels (*Aulacomya ater*), that previously made up most of the biomass on rocky shores (Branch and Steffani 2004). This has necessitated an increased reliance by African Black Oystercatchers on *M. galloprovincialis* as a food source. Male African Black Oystercatchers mainly fed on limpets and females on bivalves to reduce intra-species competition (Hockey and Underhill 1984, Kohler et al. 2009a), but since the invasion both have been found to feed on *M. galloprovincialis* equally (Hockey et al. 2003, Coleman and Hockey 2008), even though *M. galloprovincialis* offers less energy than limpet species (Coleman and Hockey 2008).

Although oystercatcher chicks are precocial they are reliant on their parents for food (Hockey 1982a). This is necessary as it requires a hard bill and learned skill to feed on bivalves and limpets (Hockey 1979). African Black Oystercatcher chicks need up to 615kJ per day to remain healthy with requirements increasing as they age (Hockey 1984). The parents thus need to use a lot of energy foraging to feed their young (Leseberg et al. 2000), as territory restrictions mean that chicks cannot always be taken directly to the prey. This is not the only factor inhibiting feeding as human collection has caused a large decrease in the rocky shore mollusc biomass (Castilla 1999) which is the reason proposed for the extinction of the Canarian Black Oystercatcher (*Haematopus meadewaldoi*) (Hockey 1987).

Conservation importance of the African Black Oystercatcher

An increase in modal clutch size is a considerable change in a species' life history due to potential effects on population size as a result of increased breeding success. As the African Black Oystercatcher is a long studied bird species it is a rare opportunity to investigate what may be causing this change. As African Black Oystercatchers are K-selected determinate layers, it is important to understand what the influencing factors may be and what affect this increase may have on the fledging rate and population growth. Clutch size increase may also be a sign of improved parental condition which, if found to be true, could be an indicator of breeding site health. These findings can then be applied to other K-selected breeders to understand clutch size changes that may be occurring.

Table 1.2: Published African Black Oystercatcher clutch sizes over the breeding range of Southern Africa

Locality	Season	Percentage of nests			n	Average	Source
		1-egg	2-egg	3-egg			
Marcus Island	1975-76	38	62	0	13	1.62	Summers and Cooper (1977)
	1979-80	18	82	0	84	1.82	Hockey(1983)
Dassen Island	1971-72	15	83	2	41	1.88	Summers and Cooper (1977)
Robben Island	2001-04	8	86	6	205	1.98	Tjorve and Underhill (2008)
	2004-05	41	59	0	73	1.59	Braby and Underhill (2008)
Koeberg	2002-03	36	64	0	78	1.64	Parsons(2006)
	2003-04	22	78	0	46	1.79	Parsons(2006)
	2004-05	38	63	0	16	1.63	Parsons(2006)
Cape Peninsula	1958-59	23	77	0	13	1.77	Hall (1959)
Cape Agulhas	1978-79	17	79	4	24	1.88	Jeffery and Scott (2005)
	1979-80	12	84	4	25	1.92	Jeffery and Scott (2005)
	1980-81	40	60	0	15	1.60	Jeffery and Scott (2005)
	1981-82	33	67	0	15	1.67	Jeffery and Scott (2005)
	1982-83	40	60	0	10	1.60	Jeffery and Scott (2005)
	1983-84	20	80	0	10	1.80	Jeffery and Scott (2005)
	1984-85	62	38	0	13	1.38	Jeffery and Scott (2005)
	1985-86	43	50	7	14	1.64	Jeffery and Scott (2005)
	1986-87	32	68	0	22	1.68	Jeffery and Scott (2005)
	1987-88	29	71	0	14	1.71	Jeffery and Scott (2005)
	1988-89	44	56	0	32	1.56	Jeffery and Scott (2005)
	1989-90	54	46	0	28	1.46	Jeffery and Scott (2005)
	1990-91	38	63	0	32	1.63	Jeffery and Scott (2005)
	1991-92	19	81	0	32	1.81	Jeffery and Scott (2005)
	1992-93	17	83	0	30	1.83	Jeffery and Scott (2005)
	1993-94	32	65	3	37	1.70	Jeffery and Scott (2005)
	1994-95	31	69	0	32	1.69	Jeffery and Scott (2005)
	1995-96	21	75	4	28	1.82	Jeffery and Scott (2005)
	1996-97	33	67	0	33	1.67	Jeffery and Scott (2005)
	1997-98	18	79	4	28	1.86	Jeffery and Scott (2005)
	1998-99	31	69	0	29	1.69	Jeffery and Scott (2005)
	1999-00	55	45	0	33	1.45	Jeffery and Scott (2005)
	2000-01	44	56	0	32	1.56	Jeffery and Scott (2005)
	2001-02	35	61	3	31	1.68	Jeffery and Scott (2005)

African Black Oystercatchers are an important species not only because of their charismatic appeal and vulnerability but also due to their effects on the intertidal zones where they occur. They are a keystone species as they alter the species ratios as well as the shell shape of their prey species (Hockey and Branch 1984), and although their population is fairly small (>6500 birds), some nesting sites support high densities of birds which require a large amount of prey to allow them to breed successfully. If the increase in clutch size is resulting in a greater number of fledglings it may cause greater competition at sites and result in alternative nesting sites and prey species which could result in competition with other species.

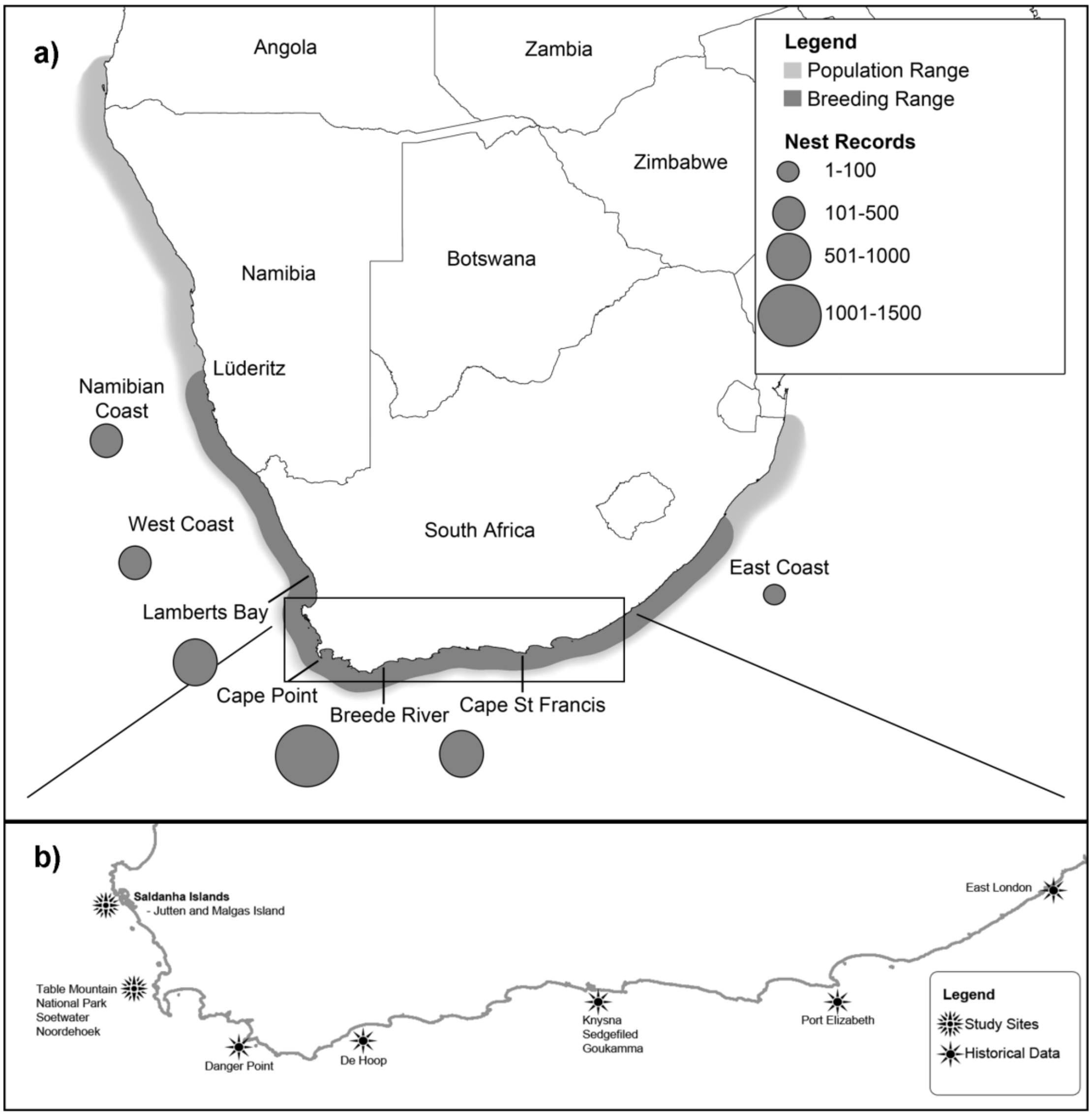

Figure 1.1: African Black Oystercatcher population and breeding range across southern Africa, showing a) coastal stretches where nest records where located as well as b) high intensity monitoring sites. Circles indicate the number of nest records per breeding zone

Aims and Objectives

The aims of this thesis are to first demonstrate that there has been an increase in frequency of three-egg clutches (Chapter 2); investigate the factors that may be responsible for this increase (Chapter 3), and then determine whether the change in clutch size affects the breeding success of the African Black Oystercatcher (Chapter 4). The thesis is presented as chapters intended to answer the key questions regarding the likely causes and results of an increase in three-egg clutches, but are written as stand-alone papers to aid in publication, consequently repetition may occur.

Firstly in Chapter 2 I establish: 1) that an increase in the frequency of three-egg clutches in the African Black Oystercatcher has occurred and, 2) assess whether the increase is focussed at particular areas along the coast. In Chapter 3, I try to identify factors that may be influencing the increase. The following three questions are investigated: 1) Are three-egg clutches a result of polygyny or egg dumping? 2) Do three-egg clutches represent a change in breeding effort in the African Black Oystercatcher? 3) Is the egg and clutch size related to the parents' body size? Initially it was planned to test parentage genetically, but this was abandoned due to incompatible primers and too few clutches where both parents were sampled. The difference in egg shape within a single nest (Mónus and Barta 2005) was therefore used as a indicator of eggs laid by multiple females. It is likely that the size of the bird is correlated to the mass of the eggs, and may also apply to clutch size as in other Charadrii (Moreau 1944a).

In Chapter 4 the incubation and reproductive success is investigated by addressing the following questions: 1) Are more hatchings/fledglings being produced by birds laying three-egg clutches than those laying two-egg clutches? and 2) can the African Black Oystercatcher incubate three eggs effectively? Although laying a third egg may result in a third chick, fledging three chicks involves considerably more effort than two chick broods. To assess the hatching and fledging success of the different clutch sizes, I compare the complete breeding season records to determine the success of each clutch size. This allows the extra investment placed in three-egg clutches to be assessed in terms of fledgling output per clutch size. As addled eggs were occasionally noted in the three-egg clutches, it is also important to assess whether African Black Oystercatchers can incubate more than two eggs, as a reduction in incubation efficiency has been posed as a possible restriction on larger than modal clutch sizes in other waders (Wallander and Andersson 2002).

This study provides an understanding of breeding site importance and will aid future conservation efforts for this species. Ultimately the knowledge gained from this study allows a better understanding of the breeding dynamics of African Black Oystercatchers and whether the change in clutch size will affect the demography of the species.

Chapter 2: Temporal and spatial differences in three-egg clutch frequency of the African Black Oystercatcher

Abstract

Historically African Black Oystercatchers naturally produce a modal clutch size of two, rarely laying three-eggs. By reviewing over 4000 nest records from across their breeding range (dating back to the early 1960s), I found that three-egg clutches have become more frequent and in recent years make up over 6% of clutches. Three-egg clutches are currently site specific and found predominantly at south-western sites, with the most change in frequency occurring within the Western Cape. They are produced earlier in the season compared to smaller clutch sizes and rarely occur after January. Due to the site fidelity it is possible that a localised change in mating habit is occurring or a heritable trait is linked to this increase. However, further research is needed to identify the cause of this phenomenon and evaluate how this change may affect the breeding success of this species.

Introduction

For many bird species, clutch size (number of eggs per female per nest) results from phenotypic plasticity and is dependent on external factors such as resource availability and female nutrient reserves (Skutch 1985, Martin et al. 2000). This is especially true for indeterminate layers which produce replacement eggs for losses sustained during incubation. For K-selected (long lived, slow reproducing) determinate layers however (e.g. sea-birds, waders and many raptors), this is not common as clutch size is genetically determined and may rather be related to a change in breeding strategy (Pianka 2008).

Oystercatchers (Haematopodidae) are determinate layers which naturally lay clutches of one to four eggs (Hockey 1996). Small clutch sizes are strongly selected for, as their precocial chicks require feeding as well as protection (Safriel 1975). African Black Oystercatchers (*Haematopus moquini*) like most of the Haematopodidae are monogamous (Kilner 2006), laying a modal clutch size of two eggs (Summers and Cooper 1977, Hockey 1985). However, there have been increased reports of three-egg clutches occurring over the last few decades (Chapter 1).

As the African Black Oystercatcher is an extensively studied species (over 50 years of monitoring records), it is possible to assess if this increase in three-egg clutches is occurring and discover in which areas it is most prominent. In this chapter I utilise historical African Black Oystercatcher nest records to identify possible temporal and spatial increases in three-egg clutches. If there is no significant change in three-egg clutch frequency I predict that the proportions of three-egg clutches will not differ between decades, years and breeding sites. Additionally I test whether clutch size varies within the breeding season.

Methods

The African Black Oystercatcher has been well studied due to its near threatened status and charismatic appeal. This has resulted in over 4000 nest records, dating back 50 years, from across their entire breeding range. These records were obtained through the Percy Fitzpatrick Institute of African Ornithology (PFIAO), Animal Demography Unit (ADU), and birding clubs/individuals. Records of nests visited at least twice (over two days apart as eggs are laid at 48 hr intervals) containing nest location, sighting dates and clutch size were analysed. Multiple visits were needed to confirm maximum clutch size (i.e. Clutch size remained constant for two successive visits). As the dataset rarely included egg measurements and mass (commonly used for laying date estimates), lay dates were estimated where possible (regularly visited sites (< every 7 days)) by establishing the midpoint between initial nest sighting date and the previous visit. This can be obtained with accuracy as African Black Oystercatchers are very territorial and maintain nesting territories which can be identified by the nest scrapes produced before the breeding commences. This was then used to calculate the number of days since the start of the season (based on the earliest recorded laying date, 10 October).

The nest records were sorted according to the coastal regions defined in Loewenthal, 2007 (Figure 1.1), year and decade to identify spatial and temporal differences in mean clutch sizes and frequency. The quarter degree grid cells where the nests were located were used to assign rough geographic coordinates. Long-term trends were calculated by correlating the percentage of three-egg clutches to years (1965-present) and decades (1970 to 2010) for the entire breeding range as well as separate regions using linear regressions. Seasonal trends were then analysed by correlating the percentage of three-egg clutches occurring within each month of the breeding season.

It is believed that geographic variation can influence the clutch size of oystercatcher species (Väisänen 1977, Nol et al. 1984). To identify if geographic (latitudinal and longitudinal) differences in clutch size occur a GLM (binomial) was performed to calculate the combined effect of latitude and longitude on the probability of three-egg clutch occurrence. A GLMM (R package glmmML v.1.0) was also performed with region as a random effect to create binomial models determining whether three-egg clutches were more likely attributed to season (day recorded after start of season) or decade. Region was a random factor in the GLMM as it was found to be a significant determinate in three-egg clutch probability, and by adding it as a random factor it was possible to calculate the correlation of clutch sizes within sites independent of geographical differences. Models exhibiting the lowest AIC value are presented in the results.

Results

African Black Oystercatchers have shown a significant increase in three-egg clutches per year ($R^2 = 0.2357$, $F = 12.64$, $p < 0.001$), and over the last four decades ($\chi^2_5 = 9.37$, $p < 0.05$) (Table 2.1). Most of this increase occurs on the southern parts of the breeding range as nests found further south-west had a greater probability of being three-egg clutches (Table 2.2). This was attributed to the probability of three-egg clutches increasing as latitude increased and longitude decreased. This increase occurred mainly from Lamberts Bay to Cape Point ($\chi^2_5 = 7.48$, $p<0.01$), Cape Point to Breede River ($\chi^2_5 = 51.48$, $p < 0.001$), and Breede River to Cape St. Francis ($\chi^2_5 = 4.44$, $p < 0.05$) (Table 2.1). Namibia and the West Coast produced no three-egg clutches and the East Coast maintained a similar frequency (4%) of three-egg clutches over the past four decades (Table 2.1). The greatest increase in three-egg clutch frequency is found between Lamberts Bay and Cape St. Francis ($\chi^2_4 = 6.58$, $p < 0.01$).

Table 2.1: African Black Oystercatcher average clutch size, and one-, two-, and three-egg composition (%) across six coastal regions of southern Africa, over the last four decades

			Percentage of nests			
Coast line	**Decade**	**Average Clutch Size**	1-egg	2-egg	3-egg	**n**
Namibia	1965-1974	-	-	-	-	-
	1975-1984	2.00	0	100	0	6
	1985-1994	-	-	-	-	-
	1995-2004	1.66	34	66	0	41
	2005-2014	2.00	21	79	0	92
West Coast	1965-1974	1.91	9	91	0	11
	1975-1984	1.90	10	90	0	20
	1985-1994	2.00	0	100	0	18
	1995-2004	2.00	5	95	0	40
	2005-2014	-	-	-	-	-
Lamberts Bay to Cape Point	1965-1974	1.89	12	87	1	92
	1975-1984	1.82	19	80	1	212
	1985-1994	2.00	0	100	0	3
	1995-2004	2.01	9	81	10	445
	2005-2014	1.78	30	62	8	124
Cape Point to Breede River	1965-1974	1.77	23	77	0	39
	1975-1984	1.85	18	80	2	253
	1985-1994	1.78	24	74	2	446
	1995-2004	1.80	24	73	4	442
	2005-2014	1.93	13	80	7	120
Breede River to Cape St. Francis	1965-1974	2.00	0	100	0	3
	1975-1984	1.77	23	77	0	26
	1985-1994	1.80	20	79	1	123
	1995-2004	1.76	26	73	2	580
	2005-2014	2.00	20	76	4	106
East Coast	1965-1974	2.29	0	71	29	7
	1975-1984	2.00	4	92	4	53
	1985-1994	1.79	21	79	0	19
	1995-2004	2.03	1	95	4	212
	2005-2014	2.04	0	96	4	112
Total	1965-1974	1.88	14	84	2	152
	1975-1984	1.85	17	82	2	570
	1985-1994	1.79	22	76	1	609
	1995-2004	1.87	18	78	5	1760
	2005-2014	1.88	17	79	5	554

Table 2.2: Estimated regression parameters (±SE) calculated through generalized linear models, predicting African Black Oystercatcher three-egg probability as a function of latitude and longitude (two- to three-egg clutches)

Parameter	**Value**	**±SE**	**t-value**	**p-value**
(Intercept)	-14.0761	4.92445	-2.858	0.00426
latitude	0.36585	0.15237	2.401	0.01634
longitude	-0.07964	0.0444	-1.794	0.07286

Unlike one- and two-egg clutches which peak in January, three-egg clutches (n=83) tend to occur earlier in the season with most occurring in December (Figure 2.1). Additionally no records of three-egg clutches were recorded after February. Further analysis validated season (days after start of season) and decade as significant parameters, with the frequency of three-egg clutches decreasing as the season progresses and increasing with decades (Table 2.3).

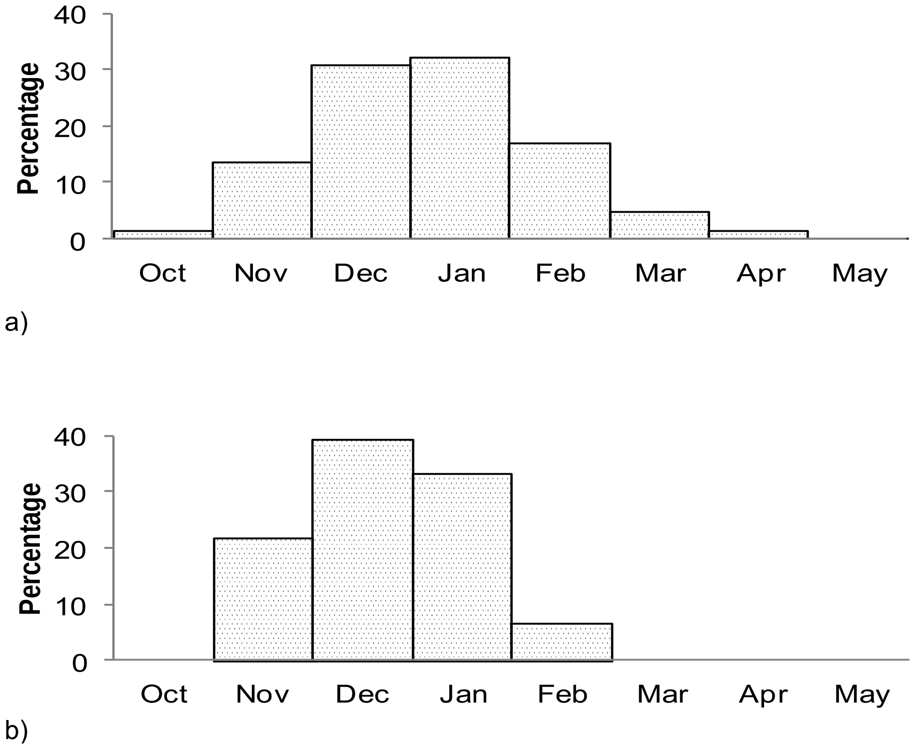

Figure 2.1: The percentage of a) one- and two-egg clutches and b) three-egg clutches occurring monthly through the African Black Oystercatcher breeding season (relays included).

Table 2.3: Parameter estimates and likelihood ratio tests of the GLMM for African Black Oystercatcher three-egg clutch frequency (probability of three-egg clutches (1=yes, 0=no)) of all localities combined

Parameter	Value	Std.Error	DF	t-value	p-value
(Intercept)	-71.252	21.634	3049	-3.294	0.001
season	-0.018	0.006	3049	-3.201	0.001
decade	0.034	0.011	3049	3.158	0.002

Random effect for GLMM = Coastline

Discussion

Temporal changes

The increased frequency of three-egg clutches from 2% pre-1975 to over 7% is a notable change for the African Black Oystercatcher. As African Black Oystercatchers are determinate layers this change in frequency could likely be attributed to a change in mating systems (Chapter 1), similar to that of the Eurasian (Heg and Treuren 1998) and Australian Pied Oystercatchers (Totterman and Harrison 2007), which produce larger clutches by forming polygynous trios. Egg dumping at these sites may also be a factor as seen in the Eurasian Oystercatchers in Scotland (Craik 2010).

Given that Charadriiformes most likely come from an ancestor which laid four-egg clutches (MacLean 1972), monogamous pairs may also be laying three-egg clutches as a result of favourable conditions (phenotypic placticity) or genetic predisposition. If pairs predisposed to lay three-egg clutches exist, they could be responsible for the higher three-egg clutch frequency due to an increase in their own breeding success. This may be aided by external factors, such as an increase in resources or decreased predation (Lima 1987, Martin et al. 2000, Loewenthal 2007). Although the increase in three-egg clutches does coincide with the invasion by the alien mussel *Mytilus galloprovincialis* this is probably not a major contributing factor because the invasion has reduced other native food sources (Branch and Steffani 2004), and *M. galloprovincialis* is a less preferable food source given its lower energy content (Coleman and Hockey 2008). Breeding pairs in Port Elizabeth have also shown no change in three-egg clutch frequencies since the introduction of *M. galloprovincialis* in 1990. Physiological factors such as bird mass and age could contribute but very few studies corroborate this relationship in determinate layers (Moreau 1944a, Haywood and Perrins 1992).

Spatial changes

A focus of three-egg clutches around the southern region of the breeding range supports theories explaining intraspecific clutch size variation as a location-based response related to resource availability and seasonal variability (Moreau 1944a, Lack 1947, Murray 1976, Dunn et al. 2000, Jetz et al. 2008). As the range of African Black Oystercatchers is fairly small this is more likely due to site fidelity (Hockey 1985) rather than ecological variation. It is interesting to note that the East Coast has had an elevated proportion of three-egg clutches since the 1970s which may imply that the occurrences originated from there and as a result of juvenile migration to the Western Cape (Hockey et al. 2003) this phenomenon spread westward.

Given that most three-egg clutches appear within the first three months of the breeding season, this may imply increased investment early on, as fitness at this time was maximised as a result of reduced competition (Verhulst and Nilsson 2008). Pairs of a higher quality also breed earlier and may be able to produce larger clutches. If resources allow, this should increase fledgling output by pairs producing three-egg clutches, therefore increasing the quantity of three-egg clutches further as juveniles exhibiting this trait return to their natal sites (Hockey 1985). They may also settle at new sites enforcing this habit there, resulting in the singular occurrences at certain sites.

Conclusions

The increase in three-egg clutches represents a significant change in the breeding pattern of African Black Oystercatchers. As the increase is currently site specific it is likely due to either a localised change in breeding strategy (polygyny or egg dumping), or an increase in pairs laying three-egg clutches (phenotypic plasticity). It will thus be important to identify which of these phenomena are occurring and determine the driving factors behind them to help understand the future impacts for this species. Chapter three will attempt to identify which of these two factors (breeding effort of strategy) are giving rise to this phenomenon.

Chapter 3: Are three-egg clutches due to an increase in breeding effort or a change in breeding strategy by the African Black Oystercatcher?

Abstract

Over the last few decades three-egg clutch frequency has increased for the African Black Oystercatcher. As this species has been a focus of study for over three decades it offers an opportunity to attempt to understand the factors increasing wader clutch size. Breeding effort in the Western Cape, South Africa was monitored over the 2011-2013 breeding seasons and combined with similar data records from across their breeding range. Behavioural observations and egg-shape comparisons suggest that polygyny and egg-dumping unlikely account for the increase in three-egg clutch frequency. This implies that an increased breeding effort by those predisposed to laying larger clutches is most likely the cause of three-egg clutches. Correlations were identified by modelling egg mass, repeat clutches and parental biometrics to clutch size and found that large clutches were related to males and females with a greater mass. Repeat clutches and total egg investment within the season have also increased for those laying three-egg clutches as producing three-egg clutches had no negative effect on initial egg mass or repeat clutch size. Further studies are needed to assess the dispersal of these pairs responsible for the increased frequency of three-egg clutches and identify changes in breeding success.

Introduction

Clutch sizes (number of eggs in a single nest) of determinate layers such as oystercatchers are genetically driven unlike the indeterminate layers which respond to changes in resource availability (Moreau 1944a, Lack 1947). This means increased clutch size in determinate layers is usually a result of changes in breeding strategy (polygyny or egg dumping). Determinate layers able to increase clutch size and breeding effort may occur, although these are uncommon and result from genetic abnormalities. Therefore, changes in modal clutch size for these species can mean a significant change in their life history.

Oystercatchers are K-selected (long lived, slow reproducing) waders that usually produce clutches of one to four eggs (Hockey 1996). Small clutch sizes are usually selected for, because unlike most other waders their chicks require feeding, as well as protection (Safriel 1975). Like most of its congeners the African Black Oystercatcher is monogamous laying a modal clutch size of two eggs (Summers and Cooper 1977). However, there has been an increase in the frequency of three-egg clutches over the last 20 years (Chapter 2). As the African Black Oystercatcher is an extensively studied species (over 30 years of monitoring records), it offers a rare opportunity to understand the underlying cause of a change in the modal clutch size of this determinate K-selected breeder.

Changing breeding strategy

As three-egg clutches are currently site specific (Chapter 2), the possible causes for their increase may be an emergence of polygyny or egg-dumping within sites. Polygyny occurs when a male breeds with two or more females either in an "aggressive" or "cooperative" group (Heg and Treuren 1998). A cooperative group which lays all the eggs within one nest will form larger clutches than that of a monogamous pair as observed with the Eurasian (Heg and Treuren 1998) and Australian Pied Oystercatchers (Totterman and Harrison 2007). Although there has been no proof of polygyny in the African Black Oystercatcher there was one reported incident of a third adult accompanying a pair at Cape Recife (Phil Wittington and Tony Tree, pers. comm.). It was not confirmed whether the third bird formed part of a trio as it was never seen incubating.

The common assessment for polygyny involves observations of breeding pairs to determine if extra females are present. In cases where monitoring is not feasible, other methods of testing polygyny, such as genetic comparison of both parents and young (Griffith et al. 2002), egg swabbing (Schmaltz et al. 2006), and biometric similarities of the eggs within a single clutch (initial mass, colour, shape, pattern, length and breadth (Barta and Szekely 1997)) can be used. These methods are also useful for identifying egg-dumping (where a female lays an egg into another females nest), which also occurs in Eurasian Oystercatchers (Craik 2010).

Increase in breeding effort

In favourable conditions, producing additional eggs should produce more offspring. As oystercatchers are determinate layers a parent would need to be predisposed to lay larger clutches (Chapter 1). This would also require additional energy reserves to produce an extra egg so only healthier birds in the population may be able to achieve it (Moreau 1944b). An African Black Oystercatcher female weighs on average 723 g (Hockey 1996) and the average mass of each egg is 55.8 g (Hockey 1982a). This means that a female laying a three-egg clutch invests 15-20% of her body mass in producing it. Laying an extra egg might negatively affect her fitness by potentially reducing her health and ability to raise the offspring (Monaghan et al. 1998). Although this extra energy cost is acceptable in most cases (Walsberg 1978), and Charadriiformes are known to produce eggs of around 14.5% of their body mass (Rahn et al. 1975), the extra nutrient requirements such as calcium are not easily replenished and will be extracted from the female's bone tissue (Patten 2007). African Black Oystercatchers usually relay following the loss of a clutch (Hockey 1982a), this can further reduce a female's mass (Hegyi and Sasvari 1998), and with up to four clutches per season, total egg mass may exceed 60% of the female's total body mass. In such cases the female might be weakened and the re-laid clutches may be of poorer quality (Heaney and Monaghan 1995). Larger females and sites which offer better resources or nest protection would make it easier to produce an extra egg and successfully raise the young and may thus be a focus of larger clutches.

African Black Oystercatchers at the southern extent of their breeding range have been found to produce an increased frequency of three-egg clutches (Chapter 2). As these cases are site specific there is reason to believe these populations have altered their breeding strategy, or are increasing their breeding effort in response to other site-dependent variables. If polygyny is resulting in the increase in three-egg clutch frequency, I predict that three-egg clutches will be brooded by cooperative polygynous groups; therefore eggs will be produced by separate females. If egg dumping is resulting in the increase I predict the intra-clutch egg shape variables and measurements will not be as consistent within the three-egg clutches as the two-egg clutches. Lastly I assess the likelihood of an increase in breeding effort and its resultant effect on egg mass and relay size over that of two-egg clutches. If increased three-egg clutch frequency is a result of increased breeding effort I predict egg size and relays will be constant between pairs, and that larger females produce the larger clutches.

Methods

Study sites and nest records

African Black Oystercatchers exhibit natal philopatry and show high fidelity to their breeding sites (Hockey 1985), where monogamous pairs maintain feeding territories that they defend throughout the year (Hockey 1985). For this study (2011-2013) sites where chosen that were easily accessible and had large populations of breeding pairs (>15 pairs). Sites known to have had recent increases in three-egg clutches were focussed on, and additional data from historical records were obtained to expand the data set (Figure 1.1). To validate clutch sizes within the historical records as well as during this study only nests visited at least twice (>4 days apart) where used. This ensured breeding pairs had enough time to produce up to three eggs (laying interval of 2 days per egg). Each egg was measured (length (L) and maximum breadth (B)) to the nearest 0.1 mm using callipers. These measurements where used to infer the initial mass (initial mass=K_w×length×breadth²) of each egg (Hoyt 1979), with Kw being the species-specific observed weight coefficient calculated using known initial egg masses. Kw was calculated to be 0.516 using 80 fresh weight records collected in Saldanha Bay between 1979 and 1980 (PAR Hockey unpublished data). Partial clutches are a possibility but as cases of partial nest predation are rare this was unlikely, and searches around nests visited was done in case of egg rejection/loss.

Polygyny and egg dumping

Polygyny and/or egg dumping have not been recorded in African Black Oystercatchers, except for the possible trio at Cape Recife (Chapter 1). Ideally, a genetic confirmation of maternity and paternity would determine whether either polygyny or egg-dumping were occurring. However, incomplete primers and difficulty of trapping both putative parents at sufficient nests meant this was not feasible (especially given the possible confounding effect of extra-pair paternity). As alternative methods, extensive field observations and intra-clutch egg shape comparisons were used to detect if an extra female may account for the three-egg clutches. Over the study period (2011-2013) three-egg clutches (23 clutches) were monitored weekly throughout the breeding season for a minimum of 30 minutes each, to observe for any signs of cooperative breeding, or unusual behaviour such as trios. In many cases the pairs were colour ringed to aid in individual identification. Observations from bird clubs, researchers and volunteers around the country were also included.

As egg dumping is nearly impossible to observe I analysed intra-clutch egg shape variation (Barta and Szekely 1997) among two- and three-egg clutches. This assumes that physiological factors within the bird are similar throughout egg production so similar shape variables will be maintained within a single clutch by a single female (Christians 2002). To do this I photographed each clutch and egg at sites visited over the study period. One side of each egg within the clutch was photographed at 90 degrees from the line of symmetry, with a Canon Ixus 95s. The macro function was used to reduce lens distortion and ensure that egg shape was maintained in the image. The method used by Mónus and Barta (2005) to obtain the outer edge of the egg (XY coordinates) using ImageJ v1.47 was adapted to include the entire egg perimeter to minimise human error. These coordinates were then imported into R 3.0.1 (R development core team, 2013) where the shape variables developed by Preston (1953) and adapted by Barta and Szekely (1997) were calculated (Figure 3.2). All egg coordinates were verified against measurements taken in the field to ensure that the photographs were not distorted and were taken at the correct angle. Clutch consistency indicators (repeatabilities) were calculated for the egg shape parameter variables C0, C1, C2, and C3 along with length, breadth and estimated initial mass of all eggs. The shape parameter variables were also compared between two-egg and three-egg clutches. To verify that the repeatabilities were indeed significant, recorded estimated initial egg masses were used to randomly create identical sized samples of simulated two- and three-egg clutches, as well as three-egg clutches containing an actual two-egg clutch assigned with a random egg. This simulated the process of egg-dumping, and one thousand simulated repeatabilities were calculated and expressed in terms of frequency. Simulations were restricted to one thousand replicates due to the long running time of the analysis.

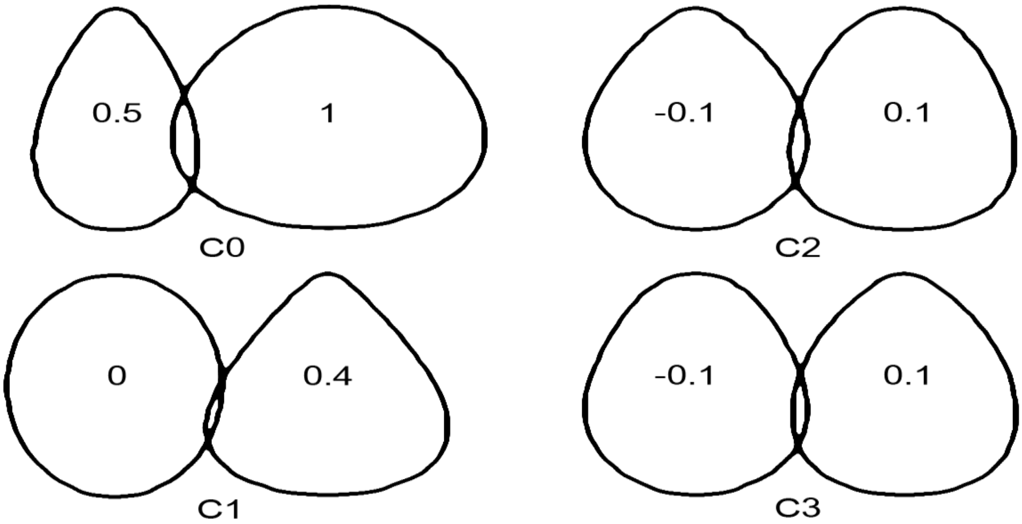

Figure 3.2: The effect of varying egg shape parameter variables (C0, C1, C2, and C3) on egg shape. Each egg shape parameter is shown with their corresponding minimum (left) and maximum (right) natural value possible for an egg. A combination of these values can be used to recreate natural egg shapes (adapted from Barta and Szekely (1997))

Breeding Effort

To compare the breeding effort of African Black Oystercatchers breeding sites (Figure 1.1) were monitored throughout the study (2011-2013), and all historical nest records were compiled (Chapter 2) to have a representative sample (both spatially and temporarily) of the entire breeding range. Study sites were visited every 3-7 days over the breeding season, and data were combined with those from nest records monitored with similar consistency. The average initial egg mass of one-, two- and three-egg clutches were compared to find out if a reduction in egg mass may be a factor in producing a third egg per clutch. African Black Oystercatchers are highly territorial and repeat clutches are laid very close to the preceding attempt (Hockey 1982b), so it is easy to identify clutches produced by each pair. This made it possible to record all clutches laid by parents and analyse the entire breeding effort over the season. As this project followed on from a long term study (13 years) utilising the same protocol, it was possible to combine all repeat clutch data into one large set. The mean estimated initial egg masses and clutch size ratios of repeat clutches for one-, two- and three-egg clutches were compared using a log-linear analysis to attempt to explain the seasonal change in clutch size (Hanssen et al. 2005), and identify if producing three-egg clutches decreased repeat clutch sizes.

Adult effect

Male and female African Black Oystercatchers were trapped on their nests using dummy eggs in walk in traps. Sexes were identified based on known differences in biometrics, eye flecks (Kohler et al. 2009b), and cloacae distension (Hockey 1981). The parent biometrics taken included; incubating mass taken to the nearest 1 g recorded with a 1 kg Pesola spring balance, wing length taken to nearest 1 mm with a stopped wing scale (flattened straitened wing method), and tarsus and culmen length to nearest 1 mm using callipers. Binomial models were created using GLMs to determine whether three-egg clutches were more likely attributed to larger parents (Male/female, mass (g), tarsus, wing and culmen length). This was done for both sexes to ensure any correlations between clutch size and parent biometrics were not as a result of site condition. General linear models (GLMs) were done for non binomial data such as the estimated initial egg mass, and egg shape parameters. Poisson general linear models (GLMs) were done for non binomial data such as the estimated initial egg mass, and egg shape parameters, to establish the effect of the altered clutch sizes. Clutch size was assigned as the determinate factor in this analysis. Models exhibiting lower AIC values were presented in the results with non-significant values being removed from the model unless they reduced the AIC value significantly (>2).

Results

Breeding strategies

There were no signs of cooperative polygyny observed out of the 23 three-egg clutches monitored during this study, as well as the additional 126 three-egg clutches recorded by other sources. Of all the egg measurement records there was very little difference in the average length (one-egg: 61.18 ± 2.17, n = 247; two-egg: 61.16 ± 1.89,n = 1866; three-egg: 61.45 ± 1.93,n = 179) and breadth (one-egg: 41.24 ± 4.25, n = 247; two-egg: 41.01 ± 1.54,n = 1866; three-egg: 41.07 ± 1.68,n = 179) between each clutch size. Eggs within clutches had very similar estimated initial masses (Figure 3.3), with the intra-clutch average difference between eggs being 2.0 ±1.6 g for two-egg clutches and 3.3 ± 1.7 g for three-egg clutches. Two of the three-egg clutches had a larger difference but this was not above that of some of the two-egg clutches (Figure 3.3). By calculating the repeatabilities of the estimated initial egg mass between two- and three-egg clutches, two-egg clutches are found to correlate strongly (R = 0.736 ± 0.049, $p < 0.001$) within the clutches (Table 3.2). A similar correlation is seen in the three-egg clutches (R = 0.508 ± 0.155, $p < 0.001$) although this is lower than that of the two-egg clutches (Table 3.2). Comparing the intra-clutch egg size and shape parameter variables (length, breadth, C0, C1, C2, C3) in this way I found that all intra-clutch variabilities except for C3 correlated significantly in the two-egg clutches, with a similar result occurring in three-egg clutches except for C1 (Table 3.2). Throughout the results three-egg clutches had a greater variability than that of two-egg clutches which is expected based on the larger clutch size and chance of variability (two-egg: n = 97; three-egg: n = 15). The estimated initial egg mass repeatability values for both the two- (1000 bootstrap, $p < 0.001$) and three-egg (1000 bootstrap, p=0.02) clutches were both out of the range random egg placement would be likely to produce (Figure 3.4). A correlation was found between clutch size and egg shape as oystercatchers were likely to produce pointier eggs when increasing from two- to three-egg clutches (larger C1 and smaller C2 value) (Table 3.3).

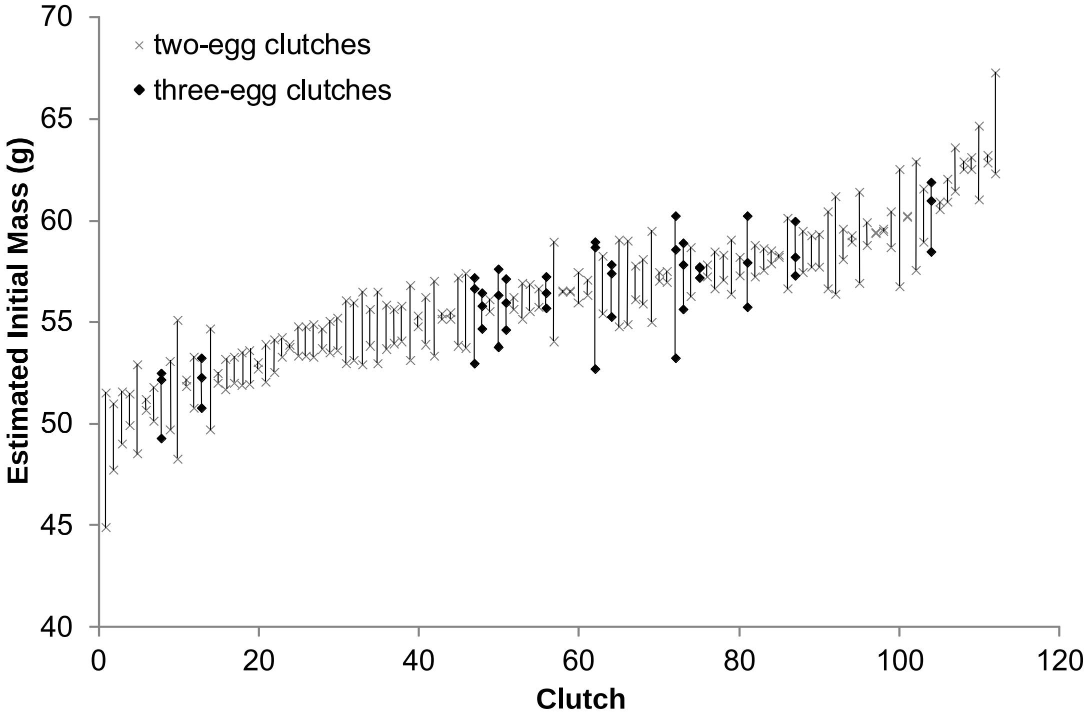

Figure 3.3: Estimated initial egg mass (g) of individual African Black Oystercatcher eggs within clutches of two-, and three-egg clutches recorded over the 2012-2013 breeding season. Clutches are ordered from smallest to largest average estimated initial egg mass

Table 3.2: Consistency indicator (repeatabilities) of intra-clutch egg size and shape parameter variables (length, breadth, C0, C1, C2, C3) and estimated initial mass for African Black Oystercatcher two- and three-egg clutches

	R	±SE	CI	P
Two-egg clutch				
length	0.764	0.043	[0.664, 0.829]	<0.001
breadth	0.585	0.068	[0.441, 0.697]	<0.001
c0	0.639	0.059	[0.510, 0.738]	<0.001
c1	0.392	0.087	[0.208, 0.552]	<0.001
c2	0.423	0.083	[0.245, 0.558]	<0.01
c3	0.230	0.095	[0.033, 0.408]	>0.1
mass[a]	0.736	0.049	[0.620, 0.815]	<0.001
Three-egg clutch				
length	0.599	0.145	[0.232, 0.795]	<0.001
breadth	0.408	0.162	[0.029, 0.701]	<0.05
c0	0.521	0.149	[0.170, 0.748]	<0.1
c1	0.000	0.091	[0.000, 0.316]	>0.1
c2	0.268	0.157	[0.000, 0.562]	<0.05
c3	0.100	0.129	[0.000, 0.418]	>0.1
mass[a]	0.508	0.155	[0.137, 0.743]	<0.001

[a] estimated from equation: $\text{mass(g)} = 0.516 \times L \times B^2$

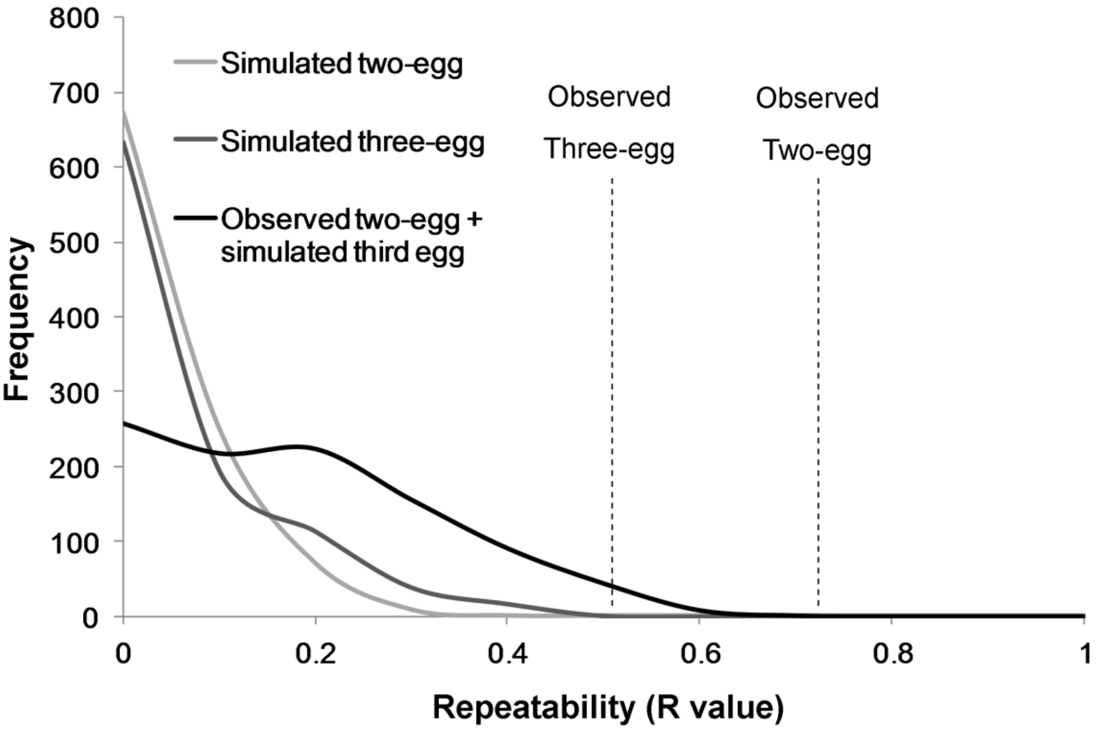

Figure 3.4: Frequency distribution of repeatabilities of intra-clutch estimated initial egg mass for clutches containing two and three randomly assigned eggs as well as samples containing actual two-egg clutches with one randomly assigned African Black Oystercatcher egg. Actual repeatability values obtained from field sampling are shown

Table 3.3: Estimated regression parameters (±SE) calculated through generalized linear models, predicting African Black Oystercatcher egg shape parameter variables as a function of clutch size (0=two- and 1=three-egg clutches)

	Estimate	±SE	t value	Pr(>|t|)
(Intercept)	0.717	1.576	0.455	0.650
l	-0.020	0.014	-1.429	0.154
b	0.040	0.033	1.210	0.227
c1	3.445	1.838	1.874	0.062
c2	-5.471	1.695	-3.229	0.001

N = 189

Increasing breeding effort

Estimated initial egg mass did not differ significantly between clutch sizes (ANOVA: $F_{3.84}$ = 1.6564, p = 0.1747) with the mean estimated initial egg mass being 54.4 ± 3.6 g (Figure 3.3). Female and male birds with a greater mass and smaller tarsus had a greater chance of parenting three-egg clutches over two-egg clutches (Table 3.4). Significant relationships were also found between larger estimated initial egg mass and a larger female tarsus and smaller culmen while no such correlation was found for any male biometrics (Table 3.4).

Table 3.4: Estimated regression parameters (±SD) calculated through generalized linear models, predicting the probability of a female or male produces a three-egg clutch.

Dependent	Fixed effect	Estimate	±SE	t-value	p-value
Clutch size	(Intercept)	5.024	1.916	2.622	0.011
	Female mass	0.006	0.002	3.077	0.003
	culmen	-0.036	0.023	-1.575	0.121
	tarsus	-0.078	0.030	-2.603	0.011
Clutch size	(Intercept)	5.260	4.619	1.139	0.262
	Male mass	0.007	0.003	2.534	0.016
	wing	-0.028	0.015	-1.917	0.063
	culmen	0.059	0.030	1.948	0.059
	tarsus	-0.068	0.050	-1.343	0.188
mass[a]	(Intercept)	56.131	12.614	4.450	<0.001
	Female culmen	-0.317	0.150	-2.118	0.039
	tarsus	0.403	0.180	2.242	0.029

[a] estimated from equation: Initial egg mass (g) = 0.516 x L x B^2

n = 132

Repeat clutches

The clutch size proportions (one-, two- and three-egg clutches) of repeat clutches were not significantly consistent ($G^2 = 32.18$, 20 d.f., $p < 0.05$) between first and second clutches ($\chi^2 = 15.71$, 4 d.f., $P < 0.005$), second and third clutches ($\chi^2 = 12.18$, 4 d.f., $P < 0.05$), and first and third clutches ($\chi^2 = 10.07$, 4 d.f., $P < 0.05$) (Table 3.5). Three-egg clutches were rarely replaced with another three-egg clutch (four records) and more frequently reverted back to the common two-egg clutch (Table 3.5). The average estimated initial egg mass was very similar for the first, second and third clutches (1st: 53.5 ± 3.5 g, n = 1242; 2nd: 53.6 ± 3.8 g, n = 495; 3rd: 53.6 ± 3.8 g, n = 53; ANOVA: $F_{3,84} = 0.782$, $p = 0.941$, 53.5 to 54.5 g). There was no reduction in estimated initial egg mass in subsequent repeat clutches of the forty five pairs which laid three repeat clutches (five produced their heaviest eggs as their first lay, nineteen produced their heaviest eggs second and twenty one produced their heaviest eggs in their third lay). Although the overall proportion of three-egg clutches decreased as the season progressed (Chapter 2), there was no significant difference between repeat clutches as three-egg clutches made up a total of 5 percent (60 records) of the first clutches, 2 percent (10 records) of second clutches and 4 percent (2 records) of third clutches (Figure 3.5).

Table 3.5: Contingency table (3x3x3) of percentage of resultant replacement clutches of one-, two-, and three-egg clutches for first, second and third clutches

		Second clutch			**Third clutch**		
	Clutch size	**1**	**2**	**3**	**1**	**2**	**3**
First clutch	**1**	1	5	0	1	7	0
	2	8	66	1	10	52	5
	3	4	15	1	7	18	0
Third clutch	**1**	0	3	1			
	2	14	58	1			
	3	4	18	0			

1st replaced by 2nd lay: n = 635; 2nd replaced by 3rd lay: n = 77;

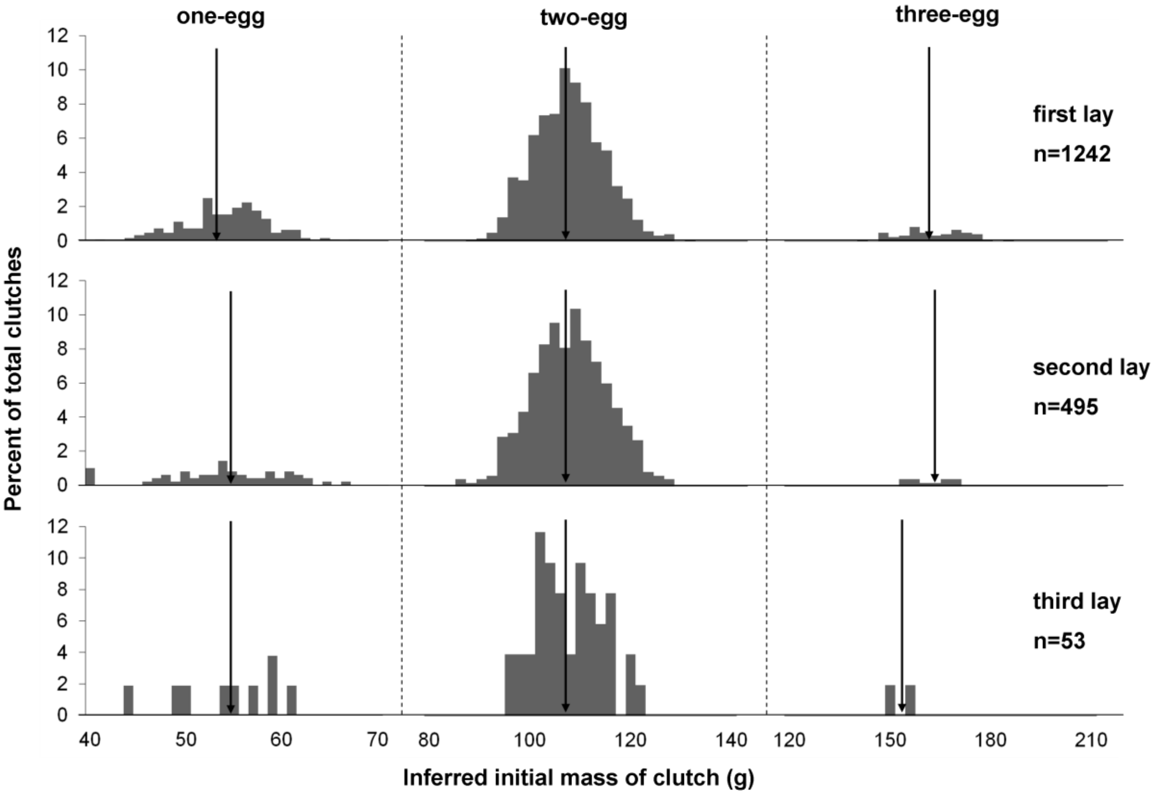

Figure 3.5: Percentage of total first, second, third clutches for each average clutch mass (g) for clutches found to be one-, two-, three-egg clutches. Mean Estimated initial clutch mass shown for each clutch size with an arrow

Discussion

Contrary to previous findings where polygyny was the source of larger than modal clutch sizes (Heg and Treuren 1998, Totterman and Harrison 2007, Craik 2010), my results show that an increase in breeding effort by monogamous pairs is resulting in the three-egg clutches produced by African Black Oystercatchers. Additionally, I found that this increase in effort is not resulting in either a reduction of egg masses or repeat clutches, compared to those of smaller clutches. For African Black Oystercatchers this was further explained by larger females producing larger eggs, and three-egg clutches being produced by heavier parents.

Polygyny

As confirmed through extensive monitoring and egg size/shape analysis I found strong evidence that cooperative polygynous groups were not the cause of all three-egg clutches. This is due to the birds being very territorial to any intrusion by rival oystercatchers other than their own offspring during the breeding period, with very few inter pair interactions occurring during this time other than territorial displays (Baker and Hockey 1984). Similar territorial conflict is seen in the monogamous Magellanic Oystercatcher (*H. leucopodus*) (Miller and Baker 1980) and the American Oystercatcher (H. palliatus) (Nol 1985). As the African Black Oystercatcher is a charismatic near threatened species, it has been monitored extensively across southern Africa, by both amateur and professional researchers. Due to this extensive monitoring, polygyny would likely have been recorded if it were occurring. Based on the observations alone, trios were not recorded in any of the birds incubating three-egg clutches.

Egg dumping

Egg dumping is not likely the cause for all three-egg clutches either, as the egg shape variables showed significant intra-clutch similarities between both the two- and three-egg clutches. The simulation showed that these similarities were significantly greater than random egg placement would allow, implying that each egg within these clutches came from the same female (Mónus and Barta 2005). There were two cases where one egg in a three-egg clutch was beyond the normal range, possibly due to egg-dumping, but this could be an abnormality in egg production as a result of lay sequence (Hockey 1982b).

With an increase in clutch size a change in egg shape was noted. The eggs within three-egg clutches had a lower C2 parameter variable, and sometimes a larger breadth and shorter length. This strengthens the argument that they are produced by one female as an optimal egg shape for a three-egg clutch is shorter and more conical (low C2) (Barta and Szekely 1997). This may indicate an adaptation to laying three eggs, from an ancestral lineage which produced four-egg clutches (Arnold 1999).

Breeding Effort

The African Black Oystercatchers are therefore increasing their breeding effort by laying three-egg clutches. The increase in three-egg frequency is likely a result of an increase in pairs predisposed to laying larger clutches. Additionally, producing the extra egg had no negative effect on average egg size as estimated initial egg masses was the same between clutch sizes. Laying an extra egg also had no negative effects on their ability to produce repeat clutches as the eggs within repeat clutches were a similar mass and size to that of the two-egg clutches. Although three-egg clutches are more common earlier in the season (Chapter 2) the percentage of repeat lay three-egg clutches was not significantly lower than that of first lay clutches.

As with other species larger females (positive correlation between tarsus and clutch size (Freeman and Jackson 1990)) were found to produce larger eggs (Thompson and Hale 1991), which may also allow for larger clutch production (Moreau 1944a). There was a positive correlation between female mass and clutch size although this is not definitive as female weights were obtained after egg production and variability in mass due to an enlarged oviduct can cause variation (Williams and Ames 2004). There was also no positive correlation between female tarsus length and clutch size. As a similar positive relationship between the males' mass and clutch size was found, the increase in parent mass may be an indicator of other factors within the site such as improved resource availability resulting in heavier birds.

As three-egg clutches occur mainly in certain areas (Chapter 2) pairs predisposed to producing larger clutches may be responding to increased resource availability or decreased predation risk (Summers and Hockey 1980). The increase in three-egg clutch frequency has been mooted to result from an increase in resource availability provided by *Mytilus galloprovincialis* as the increase coincides with the invasion (Loewenthal 2007). However the increase in *Mytilus galloprovincialis* has reduced other native food sources (Branch and Steffani 2004), and *M. galloprovincialis* was also only introduced into Port Elizabeth in 1990 after most of the three-egg clutches were recorded there (Chapter 2). Along with *M. galloprovincialis,* other invasive species such as *Semimytilus algosus* have emerged which need to be considered (de Greef et al. 2013). This means that site specific factors may be responsible for the increase in three-egg frequency. A future long term study could look at ringing juveniles from three-egg clutches to record their movement and resultant clutch sizes. A further look at the female biometrics is also needed to confirm the findings of this study. Finally further development into African Black Oystercatcher genetic primers needs to be done to aid in accurate identification of individuals for future studies.

Conclusions

Polygyny and egg-dumping are not likely to be the cause of three-egg clutch frequency in African Black Oystercatchers, as it is unlikely that multiple females are laying into single nests. As an increase in breeding effort from pairs able to lay larger clutches is occurring at specific sites the increase may be a result of improved resources which in turn results in heavier males and females. If an adaptation is taking place then I would predict that three-egg clutches should do better as a result of increased breeding success (Chapter 4).

Chapter 4 – Does an increase in clutch size translate into an increase in reproductive performance in the African Black Oystercatcher?

Abstract

The recent increase in the frequency of three-egg clutches produced by African Black Oystercatchers is the result of increased breeding effort by monogamous pairs. It is important to assess whether this increased effort results in a larger number of fledglings. Although a few pairs that laid three-egg clutches were able to rear three chicks, this is rare (2% of three-egg clutches). Overall chick production from three-egg clutches (0.31 ± 0.68 chicks fledged per breeding attempt) is not significantly greater than production from two-egg clutches (0.22 ± 0.52 chicks). Both strategies are more successful than single-egg clutches (0.03 ± 0.18 chicks fledged per breeding attempt). Factors reducing the success of three-egg clutches include inefficient incubation of three eggs, the increased risk of predation linked to the longer incubation period, and low fledging success due to the high costs of feeding and protecting an extra chick. Three-egg clutches are possibly a deleterious genetic trait being maintained due to low competition and increased resource availability at some mainland sites.

Introduction

The low global breeding success and fitness (number of young fledged) of waders (Charadrii) is usually attributed to low reproductive output and clutch loss (Boyd 1962). As waders are ground nesting, high clutch failures occur during incubation (Collias 1964) and losses during chick rearing (Boyd 1962), which may be negated by means of larger clutches offering more insurance against losses (Forbes 1990). This however may also result in high juvenile mortality, which tends to favour smaller clutches as this allows for more breeding attempts. Although uncommon in most wader species (Boyd 1962, Safriel 1975), larger clutches have been recorded to improve female fitness in Eurasian Oystercatchers (Harris 1967), Redshank (Wallander and Andersson 2002) and sandpipers (Sandercock 1997), which may further increase breeding success.

As a result of increased frequency of three-egg clutches African Black Oystercatchers have produced larger than modal (two-egg) clutches in recent years (Chapter 2). Although an increase in clutch size may result in additional fledglings, this may not always be the case, as a third egg may require extra effort to incubate and may not be cared for properly. The Eurasian Oystercatcher for example was unable to incubate successful clutches larger than a clutch size of four eggs (Heg and Treuren 1998), and a similar result may occur in African Black Oystercatchers. Brood patch area is a key factor restricting effective clutch incubation. While passerines have one large brood patch to help keep the eggs at an optimal temperature, waders (including oystercatchers) incubate by placing the eggs on either side of their bodies where they have two smaller brood patches (Arnold 1999). During incubation most avian eggs should be maintained between 36 and 39ºC (Webb 1987), and if the eggs fall below this range, embryonic development slows, and in some cases stops completely. If the temperature gets too high (>41ºC), the embryos die (Webb 1987). Consequently three-egg clutches may be less successful than two-egg clutches if incubation efficiency is reduced.

Breeding success

African Black Oystercatcher pairs have a low productivity of 0.34 to 0.42 fledglings per year on the mainland and 0.91 fledglings per year on offshore islands (Loewenthal 2007). The greater productivity on offshore islands results from the absence of mainland predators (Loewenthal 2007). Most losses occur during incubation (lasting between 27 and 39 days) (Hockey 1982a) and in the two weeks subsequent to hatching (Loewenthal 2007). The main reasons for clutch failure are nest flooding (storms and exceptional tides) (Calf and Underhill 2005, Jeffery and Scott 2005, Braby and Underhill 2007, Loewenthal 2007), and predation (dogs, mammals, birds, and snakes) (Jeffery and Scott 2005, Braby and Underhill 2007, Loewenthal 2007). Trampling by people also poses a significant threat, including off-road vehicles (now banned from beaches in South Africa) and horses (Leseberg et al. 2000, Jeffery and Scott 2005). In some cases visitors to breeding sites intentionally break or remove the eggs (unpubl. data). These threats have increased on the mainland with the increase in tourism and human habitation (Leseberg et al. 2000). Although over 70% of mainland clutches are lost (Loewenthal 2007), pairs usually relay within 20 days, to increase the chances of raising at least one chick per season (Hockey 1983).

Once the eggs hatch, the offspring take 32-46 days to fledge (Hockey 1983, Tjørve 2006). As African Black Oystercatcher chicks are fed by their parents and need up to 615 kJ per day (Hockey 1984), they require more parental effort. African Black Oystercatchers usually maintain a nesting territory that includes feeding grounds for their young such as rocky shores, although in densely populated areas, such as offshore islands, many pairs need to 'leap frog' over other territories to fetch individual food items (each mussel/limpet is less than 40 kJ (Coleman and Hockey 2008)) for the young (Hockey 1982a). This is necessary as African Black Oystercatchers are strongly territorial and if a chick crosses into another pair's territory it is attacked and occasionally even killed. So in cases where crossing another pairs' territory (leap-frogging) is needed, effort to feed chicks increases substantially. With the addition of the third egg and possible third chick the effort require to raise a brood (i.e. provide food and protection) is much higher.

As the increase in three-egg clutch frequency (Chapter 2) indicates an increase in breeding effort (Chapter 3) it is important to determine whether the extra investment is improving the fitness and breeding success of African Black Oystercatchers. The aim of this chapter is to identify if African Black Oystercatchers can incubate larger than modal clutch sizes of three eggs effectively and calculate if the larger clutches improve reproductive success/productivity by comparing chick production from two- and three-egg clutches. I assess incubation efficiency by using ‘dummy’ temperature logging eggs to identify if intra-clutch temperatures and egg incubation proportion are similar for both the two- and three-egg clutches. I compare the breeding success of pairs laying two- and three-egg clutches by calculating the hatching and fledging success as well as the average number of hatchlings and fledglings for each clutch size. Brood loss is also compared between one-, two-, and three-egg clutches.

Methods

Study site and incubation efficiency

Breeding pairs of African Black Oystercatchers were studied at Soetwater and Noordhoek beach (Figure 1.1) over two breeding seasons (2011-2012 and 2012-2013). Pairs were trapped using walk-in traps placed over the nests to record male and female biometrics (Chapter 3). The maximum length and breadth of the parent’s brood patches were measured to the nearest 1 mm using callipers to estimate the surface area available for incubation. This was then compared to half the average calculated surface area of the eggs. Over the 2012/2013 breeding season clutches were replaced temporarily (at least 24 hours) for randomly chosen nests (later removed from breeding success sample) containing two- and three-eggs with either two (6 replicates) or three (7 replicates) dummy temperature logging eggs (Madgetech EggTemp data logger (55 g, measurement range 0 to 55 ºC with a resolution of 0.1 ºC)). This was done to establish if African Black Oystercatchers could incubate three eggs as effectively as two eggs. The ‘dummy’ eggs were painted to resemble African Black Oystercatcher eggs and placed within the nests for at least 24 hours with a recording interval of 30 seconds to get a fine-scale temperature record. The pairs were observed shortly after replacement to ensure ‘dummy’ eggs were accepted. While the data loggers were in the nest the live eggs were placed in an egg incubator. An extra egg logger was placed near the nest to track the temperature experienced by unattended eggs (= control egg).

Nest attendance (incubation by a parent) was determined when at least one of the loggers recorded a temperature of over 33 ºC (Heg and Treuren 1998). Using this ‘incubated’ period, the overall proportion of time each individual logger egg within the clutch was being effectively incubated (>33 ºC) was calculated. The mean ‘incubated’ temperatures of each logger were calculated along with the minimum and maximum temperatures recorded during incubation. The temperature variability (maximum temperature difference between loggers at a given time record) between ‘incubated’ loggers within a single clutch was also calculated. ANOVAs were used to compare the nest attendance, incubation proportion, mean temperatures and temperature variability for the two- and three-egg clutches.

Breeding success/proportions

Breeding attempts for monitored pairs within this study (Chapter 2) were used to quantify the reproductive performance of one-, two- and three-egg clutches, the number of clutches (including relays), clutch size, estimated lay date, and hatching/ fledging success of each breeding pair. Eggs were measured and weighed to estimate laying date and initial mass, from length and largest breadth (Chapter 3). The overall reproductive output (eggs/fledglings per clutch) was also recorded. Although African Black Oystercatcher chicks are precocial, hatching success could still be recorded confidently as they are very territorial and young remain near the nest site. Alternatively a nest was recorded as unsuccessful if it was empty during a visit and there were no signs of chicks (lack of parental distress (as is normal during chick rearing) or feeding middens (piles of empty shells brought for a chick)). Successful fledging was recorded once the chicks could maintain sustained flight. As the chicks were colour ringed after two weeks they were easily identified during visits. Clutches utilised for the temperature logging study were not included in this analysis as this may have changed the hatching success of the eggs through embryo mortality and a reduction in predation risk. These data were combined with historical site monitoring data of pairs across the breeding range (Chapter 2). Only historical data which monitored pairs at a similar 3-7 day interval and recorded the same information over an entire site and breeding season were used.

The proportion of successful hatchlings and fledglings were calculated for each clutch size (one-, two-, and three-eggs) and expressed as the average number of chicks hatched and fledged per clutch. This was done by defining the clutch size as the user defined covariate values. The interval between visits resulted in uncertainty in nest success estimates. To correct for this the breeding success (probability a clutch will fledge at least one young (Mayfield 1961)) was analysed using the program MARK v.7.1 (Rotella 2005) by modelling hatching (33 days (Hockey 1982a)) and fledging (39 days (Hockey 1983, Tjørve 2006)) success containing clutch size as a covariate over the 72 day nesting period. Daily Survival Rate (DSR) was assumed to be constant over the incubation and nestling period, and estimated for each clutch size producing at least one hatchling and fledgling, with models selected for based on minimum AIC values. As the model requires comprehensive monitoring data (Rotella 2005) only those sites with suitable records were used (200 breeding, and 54 fledging attempts). The results for each clutch size were analysed separately as the model containing clutch size as a covariate obtained a lower AIC than models including clutch size as a covariate. Models were repeated to calculate the hatching success (probability a clutch will hatch at least one young), and overall fledging success (probability a clutch will fledge at least one young), of the monitored one-, two-, and three-egg clutches. A separate model to calculate success of one-, two-, and three-chick broods was done as the previous models only took the number of eggs in a clutch into account.

From this the total reproductive output of one-, two-, and three-egg clutches could be compared by calculating the cumulative reproductive output (Ro), by multiplying the average production of chicks by the nest success. ANOVAs were used to compare the hatching/overall fledging success, partial clutch survival and the cumulative reproductive outputs of the three clutch sizes, and post-hoc tests were then utilised to assess where the differences occurred.

Egg and chick loss

To establish the main factors of egg and chick loss for each clutch size, records which had a known cause of fatality (Loewenthal 2007) were compiled from both this study and the historical nest records. Although most causes were unknown (69% of clutch failures, 89% of brood failures), many failures could confidently be ascribed to flooding (due to tide or rain), mammalian predation (mongooses, baboons), dog predation, human caused fatalities, vehicle caused fatalities, abandonment by parents, sand burial, avian predation or other causes (dead chick/egg found but unidentified cause). The fatalities were compared for each clutch size and differences in proportions were analysed using a G-test.

Results

Incubation efficiency

The African Black Oystercatchers have two brood patches of <12 cm² on either side of their sternum, to incubate the eggs (exposed upper half area <35 cm²). This only allows for effective incubation of two eggs at a time. Two- and three-egg clutches showed similar nest attendance (two-egg clutch: 64.4 ± 21.3%; three-egg clutch: 50.8 ± 24.4%; ANOVA: $F_{3.84} = 0.56$, $p = 0.470$), although the eggs within these clutches experienced varying incubation proportion (two-egg clutch: 89.7 ± 7.7%; three-egg clutch: 63.2 ± 22.8%; ANOVA: $F_{3.84} = 15.05$, $p < 0.001$) (Figure 4.1). The birds incubating three-egg clutches favoured two eggs at a time resulting in one egg being neglected and being effectively incubated less than 20% of the total incubation time (Figure 4.2). This did not happen in the two-egg clutches, as both eggs achieved at least 75 % incubation efficiency, with most achieving between 85 and 100 % (Figure 4.2).

This variability in three-egg clutch incubation efficiency resulted in a large contrast in mean intra-clutch temperature recordings during incubation, which in some cases fell below 33°C (Figure 4.2). This resulted in the temperatures within three-egg clutches showing significantly greater variability than that among two-egg clutches (ANOVA: $F_{3.84} = 14.81$, $p < 0.001$). The minimum and maximum temperatures were more variable in the three-egg clutches compared to that of the two-egg clutches with most falling below 30°C, and in some cases below 25°C. On two occasions a single logger within a three-egg clutch exceeded 40°C while being incubated (Figure 4.2). This implied that the single egg in each case was being exposed to the sun as it correlated with the control temperature.

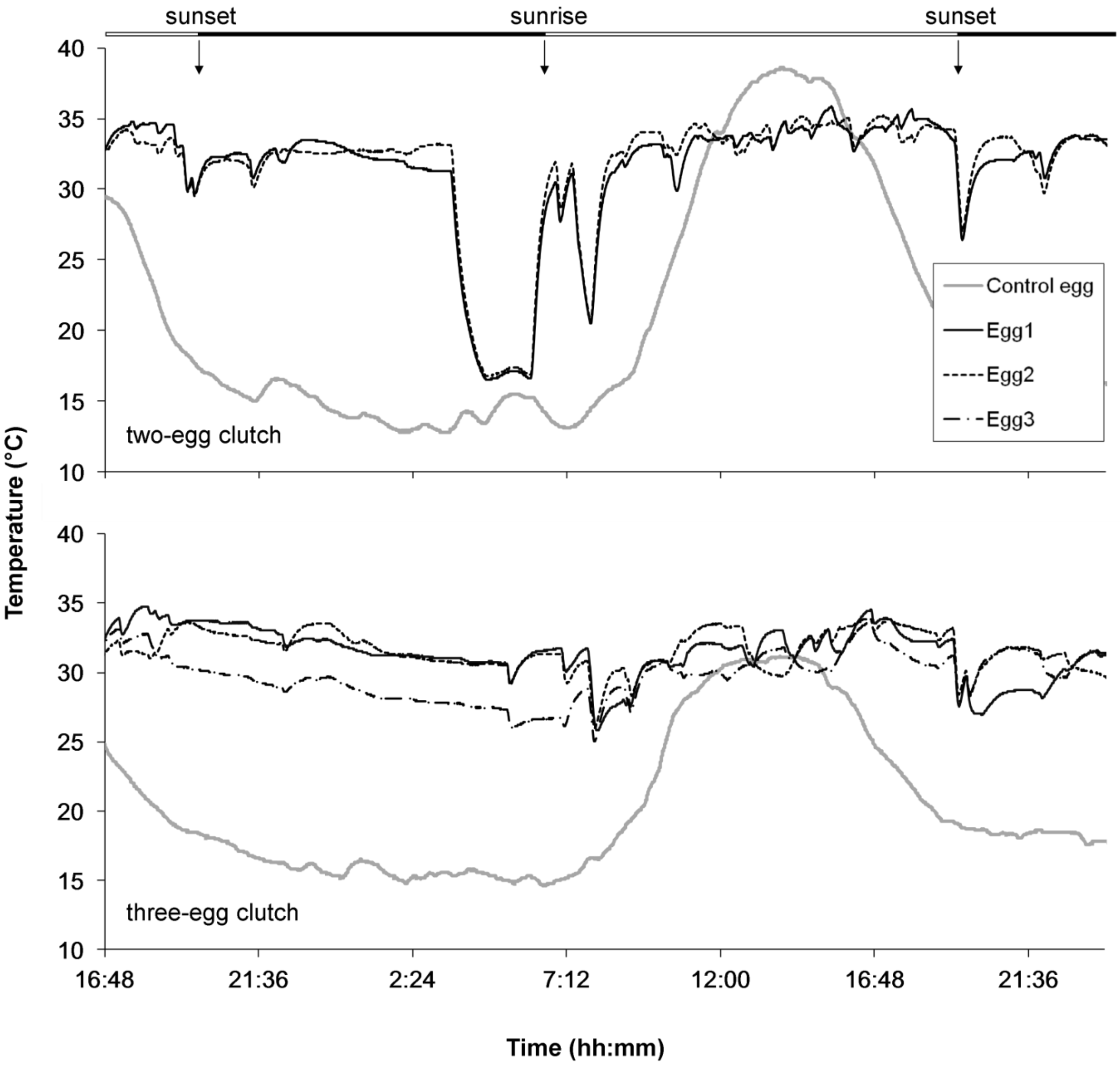

Figure 4.1: Temperature trace recorded for each 'dummy' egg incubated by the African Black Oystercatchers for a two-, and three-egg clutch. The control egg refers to the exposed temperatures

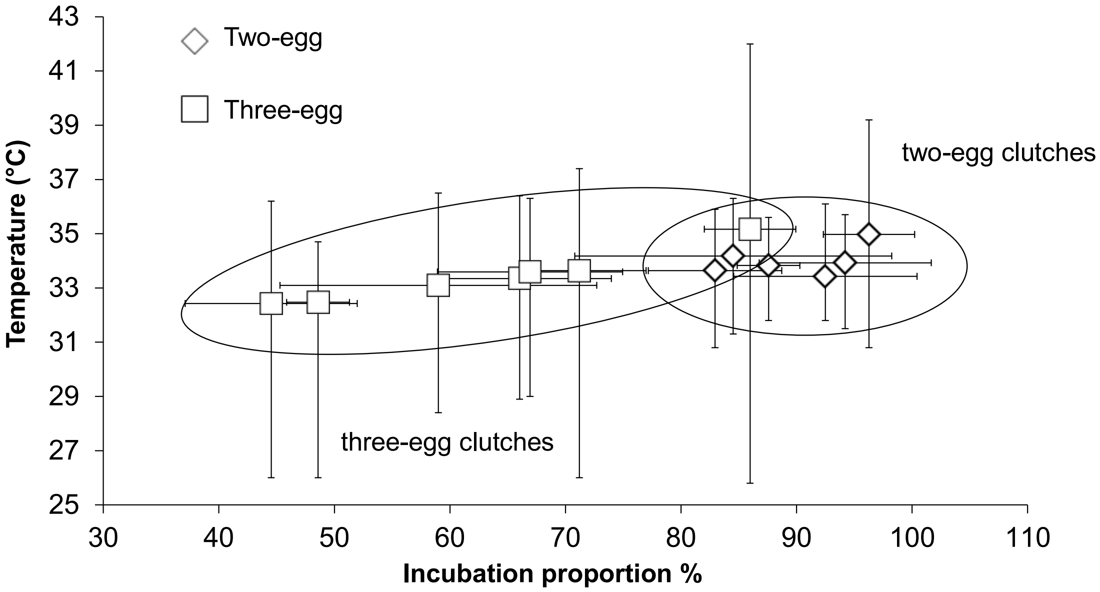

Figure 4.2: The mean (±minimum and maximum temperature recorded) 'incubated' temperature compared to the mean incubation proportion (±SD) of each clutch within 'dummy' two-, and three-egg clutches incubated by African Black Oystercatchers

Hatching/ fledging success

Of the 1924 clutches monitored for partial nest survival there were significant differences in the average number of chicks hatched (ANOVA: $F_{3.84}$ = 32.571, $p < 0.001$), and fledged (ANOVA: $F_{3.84}$ = 17.547, $p < 0.001$), from the one-, two- and three-egg clutches (Table 4.1). A Tukey HSD test showed that three-egg clutches hatched significantly more chicks per clutch (0.80 ± 1.14, n = 84) than one-egg clutches (0.14 ± 0.35, n = 400, p < 0.001) but only slightly more than two-egg clutches (0.59 ± 0.82, n = 1440, p = 0.06). A similar result was found in the average number of chicks that fledged from three-egg clutches as they raised significantly more fledglings (0.31 ± 0.68, n=84) than one-egg clutches (0.03 ± 0.18, n = 400, Tukey HSD: p < 0.001) but not significantly more than the two-egg clutches (0.22 ± 0.52, n = 523, p = 0.39). Pairs that started with a brood of three chicks produced significantly more fledgling (1.27 ± 1.19, n = 11) than one-chick broods (0.32 ± 0.47, n = 289, ANOVA $F_{3.89}$ = 36.64, p < 0.001), but the increase over two-chick broods was not significant (0.88 ± 0.79, n = 317, $F_{3.89}$ = 2.494, p = 0.115).

Table 4.1: Cumulative reproductive output (Ro)[a], daily survival (±SE), success (±SE) and average chicks hatched/ fledged (±SD) of each clutch size produced by the African Black Oystercatcher. The Ro value calculated for the hatching, overall fledging success of one-, two, and three-egg clutches, and for brood success resulting from one-, two and three-chick broods.

	Clutch size (CS)	Daily Survival Rate (DSR) [b]	Success (N) [c]	Average chicks (Ave) [b]	Ro [d]
Hatching success	one-egg	0.944±0.012 (22)	*0.161±0.068*	*0.14±0.35 (400)*	*0.0225*
	two-egg	0.960±0.004 (149)	0.272±0.035	0.59±0.82 (1440)	0.1605
	three-egg	0.957±0.012 (40)	0.249±0.033	0.80±1.14 (84)	0.1992
	Mean – 1.83 eggs	0.958±0.003 (211)	0.253±0.027	*0.50±0.80 (1924)*	0.1265
Overall fledging success	one-egg	0.945±0.027 (22)	0.018±0.090	*0.03±0.18 (400)*	0.0005
	two-egg	0.976±0.003 (149)	**0.209±0.090**	0.22±0.52 (1440)	0.0460
	three-egg	0.956±0.008 (40)	0.042±0.121	0.31±0.68 (84)	0.0130
	Mean - 1.83 chicks	0.973±0.003 (211)	**0.159±0.039**	*0.19±0.49 (1924)*	0.0302
Brood success from set brood size	one-chick	0.980±0.006 (21)	**0.457±0.113**	*0.32±0.47 (289)*	0.1462
	two-chick	0.995±0.003 (29)	**0.814±0.078**	0.88±0.79 (317)	**0.7163**
	three-chick	0.943±0.032 (4)	0.111±0.140	1.27±1.19 (11)	0.1410
	Mean – 1.55 chicks	0.988±0.003 (64)	**0.628±0.073**	*0.63±0.73 (617)*	0.3956

[a] Cumulative reproductive output (Ro) = N x Ave

[b] Number of records used for calculation in brackets

[c] Success (hatching/ fledging) (N) = $\text{DSR}^{\text{number of incubation/ brooding days}}$

[d] Values in bold and italics are significantly above and below that of the three-egg clutches respectively

Of the 200 clutches monitored for hatching/fledgling success (probability a clutch will hatch/fledge at least one young) the one-, two- and three-egg clutches varied significantly for both hatching (ANOVA: $F_{3.89} = 77.294$, $p < 0.001$) and fledgling (ANOVA: $F_{3.89} = 183.9$, $p < 0.001$) success (Table 4.1). The hatching success (proportion of clutches producing at least one chick) of three-egg clutches was significantly higher than one-egg clutches but did not differ from that of two-egg clutches (Table 4.1). The fledging success (proportion of hatchlings fledged) of three-egg clutches differed from both the one- and two-egg clutches significantly (Table 4.1). The overall breeding success (proportion of clutches producing at least one fledgling) of three-egg clutches was consequently significantly lower than that of the two egg clutches (two-egg clutch: 0.209 ± 0.090; three-egg clutch: 0.042 ± 0.122; t-test: $t_{1.655} = 7.042$, $p < 0.001$) and no different to one-egg clutches (one-egg clutch: 0.018 ± 0.090; three-egg clutch: 0.042 ± 0.122; t-test: $t_{1.655} = 0.912$, $p < 0.183$) (Figure 4.3). The success (N) of pairs that started with a brood of three chicks was not significantly different to one-chick broods (ANOVA: 0.111 ± 0.280 vs 0.457 ± 0.517; $F_{3.89} = 1.65$, p = 0.212), but significantly less than two-chick broods (ANOVA: 0.111 ± 0.280 vs 0.814 ± 0.420; $F_{3.89} = 5.39$, p = 0.007) (Table 4.1).

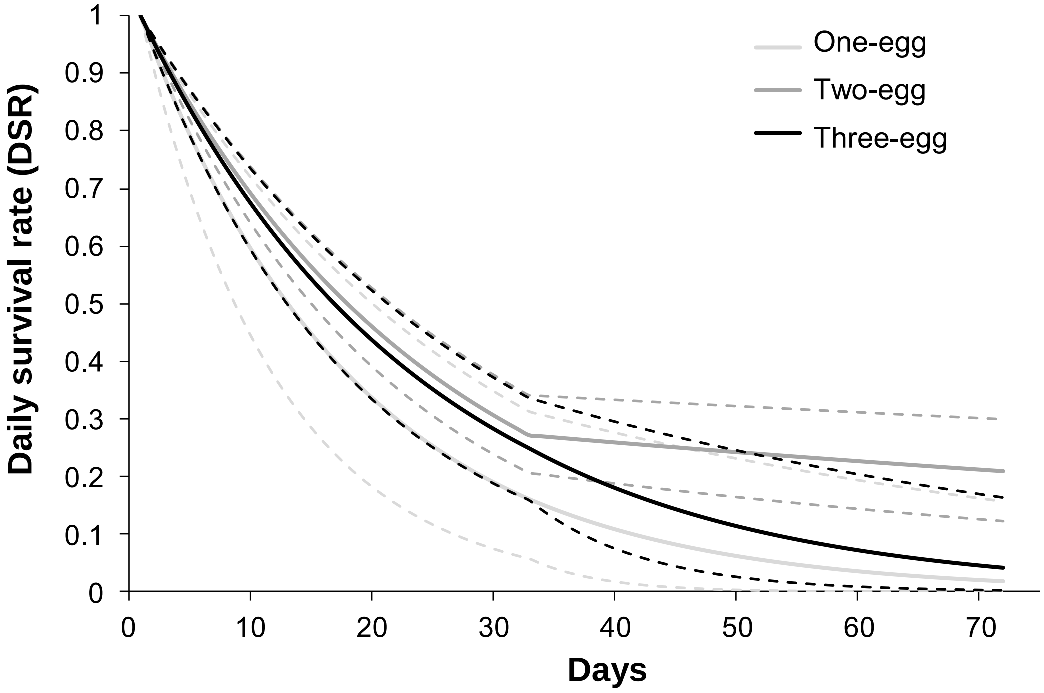

Figure 4.3: Estimated African Black Oystercatcher daily survival rate over time (days) for one-, two-, and three egg clutches (expressed for a 33 day incubation, and 39 day brood period). Dotted lines show the 95% confidence limits.

The estimates of cumulative reproductive output (Ro) produced similar results to the success (N) and average chick production values (Table 4.1). For hatching success three-egg clutches had a significantly higher cumulative reproductive output than one-egg clutches but again did not have a significant difference to two-egg clutches (Table 4.1). The cumulative reproductive output of two-egg clutches was however significantly higher than the three-egg clutches for fledging and brood success. This meant that overall two egg clutches were the optimum clutch size in terms of reproductive success.

Causes of egg/chick loss

Only 30.6% of 4062 clutches monitored had known causes for egg loss. Most of these eggs were lost due to flooding/tide (59%), while other cases represented much smaller proportions (<10%) distributed amongst the other factors (Table 4.2). The fates of the one-, two-, and three-egg clutches were not significantly similar ($G^2 = 156.3$, 20 d.f., $P < 0.001$). This was a result of three-egg clutches being destroyed by flooding less than the other two clutch sizes and mammals resulting in a large portion of the losses (Table 4.2). Sand burial and addled eggs were found to affect three-egg clutches more than smaller clutch sizes (Table 4.2). Egg loss was also recorded in cases where chicks died while hatching which was recorded predominantly in the three-egg clutches.

The cause of chick loss was only known for 11% of records. Flooding/drowning was again responsible for most fatalities (73%) accounting for the deaths of all chicks from one-egg clutches (Table 4.2). The chicks from three-egg clutches were killed by sand burial/wind more often than chicks from two-egg clutches ($G^2 = 92.18$, 12 d.f., $P < 0.001$) (Table 4.2). On high density sites such as Jutten I also recorded a number of seemingly unharmed dead chicks within the territories of pairs feeding a single chick which may indicate starvation.

Table 4.2: The estimated causes (%) of African Black Oystercatcher egg clutch and chick brood fatalities for one-, two- and three-egg clutches. Most causes were unknown (69% of clutch failures, 89% of brood failures). Only the nests where the cause could be inferred confidently were reported.

	Flood	Mammal	Dog	Human	Vehicle	Abandoned	Sand burial /Wind	Addled eggs	Avian	Other	n
Egg fatalities											
One-egg	71.1	5.9	0.0	2.6	1.3	8.6	2.0	1.3	5.3	2.0	152
Two-egg	63.6	7.7	1.4	2.8	6.0	9.7	1.4	2.4	1.6	3.2	987
Three-egg	43.5	26.9	1.9	2.8	1.9	6.5	5.6	6.5	0.9	3.7	108
All clutches	62.8	9.1	1.3	2.8	5.1	9.3	1.8	2.6	2.0	3.1	1247
Chick fatalities											
One-chick	100	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	7
Two-chick	58.7	9.1	5.8	7.4	5.8	5.0	0.8		1.7	5.8	121
Three-chick	60.0	0.0	0.0	6.7	6.7	0.0	20.0		0.0	6.7	15
All clutches	60.9	7.7	4.9	7.0	5.6	4.2	2.8		1.4	5.6	143

Discussion

Similar to other studies of African Black Oystercatchers (Hockey 1982a, 1996, Leseberg et al. 2000, Vernon 2004, Braby and Underhill 2007, Loewenthal 2007, Scott et al. 2011), the overall reproductive success and chick production was low. I was able to confirm that the production of larger clutches may not improve immediate chick production in wader species (Boyd 1962, Safriel 1975), and in some cases can even reduce the likelihood of breeding successfully. This is attributed to inefficient egg incubation at the nesting stage and the inability to protect and feed larger broods.

Incubation efficiency

Incubation of two-egg clutches by pairs was effective, maintaining both eggs at a constant optimum temperature. Three-egg clutches however were not incubated as effectively, with irregular incubation proportions, and temperatures varying more than 3 ºC between eggs within a single clutch. Similar results were found by increasing clutch sizes of the European Oystercatcher (Heg and Treuren 1998), which were unable to cope with the extra eggs. The eggs within African Black Oystercatcher three-egg clutches were frequently exposed to extreme temperatures that might result in either growth abnormalities or death (Webb 1987). The inefficiency of incubating three eggs as opposed to two implies that African Black Oystercatchers may have difficulty incubating the extra egg due to limited brood patch surface area. As each of the two brood patches only has space for one egg, it would mean the parents would need to rotate the eggs carefully to ensure they are all equally incubated. This is known to occur in more experienced wader pairs which arrange the eggs within clutches to maximise brood patch contact (Barta and Szekely 1997). Species that produce larger clutches may be aided by a larger brood patch to egg ratio or may possess multiple brood patches in to allow effective incubation (Winkler and Walters 1983, Wiebe and Bortolotti 1993) (Table 1.1), but even these species will be limited.

Inefficient incubation may be the cause of chicks from three-egg clutches dying during hatching. This can occur when pairs offer inefficient temperature control which results in insufficient water loss (Arnold 1999). African Black Oystercatchers are known to spend several hours off their nests at night to feed (Adams et al. 1999), but this extended exposure increases the eggs rate of water loss (Ar 1991), allowing desiccation to occur (Ar and Rahn 1980). Alternatively, an insufficient air sac may result in the chicks dying before or during hatching (Ar and Rahn 1980). Efficient incubation is thus vital to the chicks' early development.

Although reductions in egg temperature are not as detrimental as overheating, it is important to have an even temperature over the last two weeks of development as this is when the embryos are most at risk (Webb 1987). Irregular incubation may result in hatching asynchrony as development slows at cooler temperatures (Webb 1987). As the young are precocial, the hatching dates need to be synchronised so that all the chicks hatch together. If they are not synchronised, parents may abandon un-hatched eggs (Tjørve 2006) to spend more time protecting and feeding the other hatchlings. Addled or abandoned eggs were occasionally noted during site monitoring. However as three-chick broods occasionally fledged, some pairs were able to incubate and synchronously hatch three chicks.

Hatching success

The reduced incubation efficiency of three-egg clutches may have resulted in their lower than expected chick production. The similar chick production (average number of chicks per clutch) and reproductive output between two- and three-egg clutches was primarily due to successful three-egg clutches only producing brood sizes of one or two chicks, while two-egg would regularly hatch both eggs. Although this may result from partial nest predation it is more likely that two of the eggs were favoured during incubation resulting in failure of the third. This favouritism could subsequently expose all the eggs within the clutch to extreme temperatures over the course of incubation. This may result in the documents cases of entire clutches being addled in this study.

This reduced incubation efficiency may therefore explain the increased cases of addled eggs and sand burial within three-egg clutches. Addled eggs and burial in sand may be closely related as once an entire clutch is addled the parents may abandon it which would leave it to be buried. Although flooding was the major cause recorded for clutch loss it is also the easiest to identify so the number of records may be skewed towards it. The increased cases of mammalian predation on three-egg clutches over that of two-egg clutches may result from the fact that oystercatchers only start incubation once the clutch is complete, so during this extended exposure three-eggs may be more susceptible to predation.

Fledging success

The complete loss of clutches resulting in the low overall fledging rate of the African Black Oystercatcher is common (Hockey 1982a, Leseberg et al. 2000, Vernon 2004, Braby and Underhill 2007, Loewenthal 2007, Scott et al. 2011). A major cause of death for three-egg clutches tended to be sand burial due to wind which could imply that these chicks were weaker and possibly underfed. This may be due to parents' inability to cope with the additional energy cost of protecting and feeding additional chicks. As oystercatcher chicks exhibit sibling rivalry (Elwell and Underhill 2008, Tjørve and Underhill 2009), the weaker siblings starve, which is the likely cause of the dead chicks found at certain sites. Similar losses are experienced in 'leap frogging' Eurasian Oystercatchers (*H. ostralegus*) that are unable to retrieve enough food to feed their chicks (Ens et al. 1992).

Surprisingly two- and three-egg clutches produced a similar average number of fledglings. This is unusual as the overall breeding success of pairs laying three-eggs was significantly lower than that of the two-egg clutches. This means that most pairs laying three-egg clutches produced no offspring, while a few successful pairs produced more than one chick each. This would rely on certain pairs being significantly more successful at breeding (Harris 1967, Sandercock 1997, Wallander and Andersson 2002) as well as having better quality territories offering greater resource availability. The two three-chick broods that have fledged all three chicks to date were located at low-density sites with little interspecific competition for resources and territory. These sites also had few predators and constant human supervision which meant the young could be safely led to feeding territories (e.g. Thesen Island, Knysna).

This study therefore shows that only wader pairs able to successfully incubate, feed and protect larger clutches will improve their fledgling output through the increase of clutch size.

Otherwise this increase may only serve as an insurance (Forbes 1990) against loss or potentially decrease the chances of breeding success.

As the increase in three-egg clutches in African Black Oystercatchers is a recent anomaly, most pairs haven’t had experience raising these larger clutch sizes. With experience, these pairs may be able to successfully incubate more eggs as well as raise a larger proportion of the hatchlings. Future studies may thus need to look at the pair’s age as a factor for breeding success and monitor the birds over the long term to identify if their parenting skills are improving. This may become a positive trait producing larger brood sizes than that of the two-egg clutches.

Conclusions

By increasing their breeding effort and producing a third egg, most pairs of African Black Oystercatchers have not increased their breeding success or fledgling production above that of two-egg clutches. As the third egg reduces the pairs’ ability to incubate efficiently, three-egg clutches may even reduce total breeding success as many clutches are lost due to addled eggs. In cases where the pairs do hatch all three-eggs, they are still unable to fledge them all due to insufficient protection or feeding.

Chapter 5: General discussion

This chapter summarises the implications of my study for understanding the current increase in clutch size among African Black Oystercatchers, with a view to a more general theory of why other determinate layers may experience similar changes in clutch size. The methods and concepts within the study are presented for use among other wader species. Potential future research is proposed to help understand the restricted clutch size of both the African Black Oystercatcher and other wader species.

Purpose of study

Most waders are determinate layers and as their clutches are usually restricted to 2-4 eggs it is important to understand factors both restricting and increasing egg numbers. In this study I first confirmed that there had been an increase in clutch size among African Black Oystercatchers (*Haematopus moquini*), then attempted to determine the factors influencing clutch size in this and other wader species Determinants of clutch size among waders are poorly understood, so this offered a rare opportunity to expand on current knowledge and identify potential drivers of clutch size. Potential determinants of wader clutch size include; resource availability (Loewenthal 2007), geographic (Väisänen 1977, Nol et al. 1984) and seasonal variation (L'Hyver and Miller 1991, Rowe et al. 1994), predation risk (Summers and Hockey 1980), female physiological factors (Nol et al. 1997) and breeding strategy (polygyny and egg dumping) (Heg and Treuren 1998, Totterman and Harrison 2007, Craik 2010).

African Black Oystercatchers are an important keystone species within the rocky shore environment of southern Africa (Hockey and Branch 1984). It was thus important to understand the affect the increase in clutch size was having on the breeding success and fecundity of this species to determine what subsequent effects it may have on the population and community structures. Numbers of African Black Oystercatchers have increased in recent decades due to factors including habitat protection, increasing food stocks (Loewenthal 2007) and resultant increased breeding success (Tjørve and Underhill 2006). Therefore it is important to understand what effect the increase in clutch size may have at the affected sites.

Outcomes of the study

The data utilised for this study were collected over a large portion of the African Black Oystercatcher breeding range. This allowed for the increase in three-egg clutch frequency of this species to be validated across many of the southern breeding sites from Lamberts Bay to Cape St. Francis. Records of three-egg clutches increased from around 2% in the 1970s to over 7% in the last decade (Chapter 2). The East Coast however did not show this trend, having a consistent three-egg clutch frequency of 4% over the last four decades, with most records occurring around Port Elizabeth. The regional increase in three-egg clutch frequency over the last three decades confirmed that a change in breeding habits had occurred, so I then tested whether polygyny, egg dumping and/or increasing breeding effort accounted for the observed change.

Breeding strategies

While many bird species are monogamous, changes in breeding strategies have occurred within small groups where populations adapt to changing conditions. Changes in mating habits (polygyny and egg dumping) can arise due to territory restrictions in areas of increased populations or as a method to improve breeding success (the probability that a clutch will fledge at least one offspring) over that of other monogamous pairs (Trivers 1972). An increase in clutch size due to egg-dumping by other females is easily detected in determinate layers such as waders, as their clutch sizes are adapted to optimise fitness (Brockelman 1975) and rarely deviate from the modal size. The increased frequency of three-egg clutches produced by African Black Oystercatchers (Chapter 2), may indicate a similar change in strategy to that reported for polygamous Eurasian and Australian Pied Oystercatchers (Heg and Treuren 1998, Totterman and Harrison 2007). This inference was supported by anecdotal evidence of a third adult accompanying a pair at Cape Recife (Phil Whittington and Tony Tree, pers. comm.).

Polygyny was rejected however after extensive monitoring of three-egg clutches at Soetwater and Noordehoek revealed no signs of cooperative polygyny; all three-egg clutches were only brooded by monogamous pairs (Chapter 3). This did not eliminate the possibility of egg-dumping, as reported in Eurasian Oystercatchers (Craik 2010), as this is very difficult to detect through observation. Initially I attempted to identify egg dumping as well as polygyny by utilising genetic comparisons between parents and young to confirm maternity (Griffith et al. 2002), but microsatellite primers were not sufficiently variable and the samples sizes were too small to pursue this approach. Instead similarities in intra-clutch egg shape variables were used to verify that all eggs came from a single female, based on the premise that eggs laid by the same female will have similar shapes and sizes. The method of calculating egg shape variables developed by Preston (1953) and adapted by Barta and Szekely (1997), confirmed that most if not all three-egg clutches were the product of a single female (Chapter 3).

Breeding effort

Having concluded that most if not all three-egg clutches were produced by monogamous pairs, and given that investment in subsequent clutches did not differ between three-egg and smaller clutches (Chapter 3), larger clutches apparently represent an increase in breeding effort by some pairs. However the extra energy invested by females to lay an additional egg does not produce any net benefits (see below). Although this increased breeding effort is possible for larger females with greater energy reserves (Moreau 1944a), few records exist for determinate layers (Hegyi and Sasvari 1998). African Black Oystercatcher females producing three-egg clutches averaged heavier than those laying two-egg clutches, but there was no difference in tarsus and culmen length, suggesting females producing three-egg clutches are not larger per se but rather well-nourished (Chapter 3). Indeed, males showed a similar correlation between mass and clutch size, implying that pairs laying three-egg clutches have access to more resources, which accounts for their greater mass to tarsus ratio. Thus pairs maintaining high yielding territories may have a greater chance of producing three-egg clutches (Ens et al. 1992).

As oystercatchers are determinant layers, pairs producing larger clutches may differ genetically (or epigenetically (Allis 2007)). Resources are probably a restricting factor, and three-egg clutches may be a result of phenotypic plasticity which allows for additional eggs in high quality sites. This may be a reason for the negligible numbers of three-egg clutches being found at high-density island sites, as the territory condition would not support this additional effort (Skutch 1985, Martin et al. 2000, Figuerola and Green 2006). If this is a genetic trait however the site fidelity of juvenile oystercatchers would somewhat restrict the transfer of the trait among the population which, apart from resource availability, could explain the site-specificity of three-egg clutches (Hockey 1985). Individuals carrying this trait may have also spread stochastically from the east coast (Chapter 2) to breeding sites in the Western Cape (Hockey et al. 2003).

Hatching success and incubation

It is important to assess whether the increase in breeding effort resulted in increased breeding success and fecundity (Chapter 4). Three-egg clutch hatchling numbers and hatching success were not significantly different to that of two-egg clutches, even with this added investment. This is unexpected, because natural selection should only favour an increase in breeding effort if it confers some advantage over two-egg clutches (MacLean 1972). A larger clutch size might be beneficial if the extra egg acted as an insurance against others being lost (Forbes 1990), but partial clutch loss is uncommon during incubation in African Black Oystercatchers. Furthermore the egg fatalities of three-egg clutches were primarily addled eggs, mammalian predation and sand burial (Chapter 4). The extra mammalian predation can be explained by the extended laying time of three-egg clutches (1 egg every 2 days), but the addled eggs and sand burial is likely a result of inefficient incubation as seen in species laying larger than modal clutch sizes (Lack 1947, Heg and Treuren 1998, Lengyel et al. 2009). This means that the extra egg is likely to be negatively affecting the hatching success.

I tested whether larger clutches reduced incubation efficiency (Arnold 1999, Lengyel et al. 2009), by monitoring, two- and three-egg clutches using Madgetech EggTemp data loggers. The variability of both the incubation proportion, and temperatures was far greater in the three-egg clutches than that of the two-egg clutches (Chapter 4) suggesting three-egg clutches were not incubated evenly. Their more frequent exposure to extreme temperatures was likely cause of addled eggs and subsequent abandonment (Chapter 4).

Fledging success

As a few three-egg clutches did hatch three chicks, some pairs are able to incubate all three eggs effectively (Barta and Szekely 1997). However, there were only two records of all three chicks fledging. As African Black Oystercatchers chicks are fed by their parents, extra chicks require a greater expenditure of energy (Winkler and Walters 1983). It also results in sibling rivalry which has been known to result in the deaths of chicks due to excessive aggression (Elwell and Underhill 2008, Tjørve and Underhill 2009). This is the probable cause for the reduced reproductive output (breeding success x average no. of chicks) of three-egg clutches compared to that of two-egg clutches (Chapter 4). However, the average number of chicks fledged from three-egg clutches did not differ significantly from that of two-egg clutches, meaning that the few pairs that do successfully fledge chicks from three-egg clutches raise more chicks than pairs that have smaller clutches. This lends some support to the idea that more experienced pairs (or those with well-positioned territories) are more able to raise a larger number of chicks. Most of the records for chick loss within three-egg clutches came from flooding, wind and sand burial. These deaths are likely related to malnutrition and exhaustion as a result of apathetic parental care. The lower overall reproductive output of three-egg clutches may also be due to parental fatigue and increased predation due to increased visibility of larger broods (Safriel 1975).

Implications for wader clutch size

The increased frequency of African Black Oystercatcher three-egg clutches is an important phenomenon as it allows for the study of wader clutch sizes in a natural environment without the need for the experimental clutch size manipulation used in similar studies (Boyce and Perrins 1987, Sandercock 1997, Wallander and Andersson 2002, Larsen et al. 2003). The substantial historical dataset offers a rare chance to analyse how clutch size can vary in a wader. Furthermore it is possible to analyse the effects that this change in clutch size has on the overall breeding success and population growth without any of the negative influences of clutch manipulation.

Historically, the modal clutch size of African Black Oystercatchers has been restricted to two eggs. Increases in clutch size apparently do not improve hatching success and decrease overall fledging success (Chapter 4). This confirms numerous studies which obtain the same result through clutch size manipulation (Sandercock 1997, Arnold 1999, Wallander and Andersson 2002), which means that small clutch sizes in waders optimise the production of fledglings. The restricting factors of clutch size at the nesting stage were determined to be incubation inefficiency and increased predation of the larger clutches, while at the chick brooding stage restricting factors were related to the high energy cost of feeding and protecting larger broods.

Three-egg clutches apparently were laid by individuals predisposed to produce larger clutches. Even though it is unusual for a species to maintain a negative trait that utilises more parental effort, this may be a result of insufficient competition or a resource surplus at low-density mainland breeding sites. This could imply that species with very low populations may maintain negative traits due to partial success, which may allow for these traits to occupy a greater proportion of the population as migrants inhabit unoccupied breeding sites.

The methods adapted here may be utilised for future studies as they are particularly applicable to the field of wader reproduction. The methods in Chapter 3 used to test for the presence of polygyny and egg-dumping are useful for studies where genetic comparisons are not possible. The experimental approach developed in Chapter 4, whereby the nests where switched for egg-shaped temperature loggers, can be utilised broadly for testing incubation efficiency of regular or experimentally enlarged nests.

Future Research

Overall, three-egg clutches appear to have no net benefit compared to two-egg clutches in African Black Oystercatchers. Although it is likely to just be a negative trait it is still important to understand if there are any other drivers behind the production of three-egg clutches such as human-introduced toxins or effects which may alter hormones during breeding (Carere et al. 2010). As these larger clutches are energetically expensive and offer no benefit, further increases in three-egg clutches may negatively affect the females, reducing their fitness. It is therefore important to continue monitoring these pairs and to potentially analyse water quality, prey abundance and test for hormonal abnormalities from blood samples at sites where three-egg clutches are most frequent. Other wader species also should be monitored at these sites to identify if other species are experiencing a similar increase in clutch size.

A further analysis could also establish whether this phenomenon is occurring in secondary generations and if the trait is sex-biased, by ringing and monitoring juveniles of three-egg clutches to establish if they also produce three-egg clutches. This study would need to be undertaken over a longer period as oystercatchers are slow breeders, but it would be interesting such a study it could trace the dispersal of three-egg clutches over the breeding range. As full genome sequences become less expensive it may even be possible to relate the three-egg clutch producers over the entire range and identify which sequences code for clutch size.

Conclusions

To sum up the findings of this thesis, three-egg clutch production probably is a result of phenotypic plasticity and potentially resource-driven. This additional investment yields little or no benefit for the breeding success of African Black Oystercatchers. These findings may be directly applicable to other wader species and may help understand the selection of clutch sizes by populations to optimise breeding effort in response to external forces.

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Appendix 1: The mean egg temperature and proportion of time spent incubating each egg within the ‘dummy’ two- and three-egg clutches (at least one egg in clutch > 33ºC)

Temperature (°C)																Effective incubation proportions of each egg (%)		
Mean	**SD**	**Mean**	**SD**	**Egg 1**	**SD**	**Max**	**Min**	**Egg 2**	**SD**	**Max**	**Min**	**Egg 3**	**SD**	**Max**	**Min**	**1**	**2**	**3**
Two-egg clutches																		
35.0	6.7	96.3	4.0	34.5	6.4	37.8	17.6	35.4	7.0	39.2	16.7					93.5	99.1	
33.6	4.2	82.9	5.8	33.6	4.2	35.9	16.0	33.7	4.2	35.2	15.8					78.9	87.0	
33.8	4.4	87.6	2.7	33.8	4.2	35.6	26.0	33.8	4.7	35.5	26.3					85.7	89.5	
33.4	1.9	92.5	7.9	33.2	1.9	35.6	22.7	33.7	1.9	36.1	23.5					86.9	98.1	
34.2	1.3	84.5	13.7	34.4	1.3	36.0	29.1	34.0	1.4	36.3	28.8					94.2	74.8	
33.9	6.6	94.2	7.4	33.5	6.4	34.2	16.9	34.4	6.8	35.7	16.1					88.9	99.5	
Three-egg clutches																		
35.2	8.2	86.0	8.0	35.9	8.6	42.0	15.9	34.8	8.2	40.3	16.3	34.9	7.8	39.6	16.8	83.8	79.3	94.9
33.6	6.8	71.2	5.4	33.6	7.0	36.8	13.0	33.5	6.7	34.9	13.2	33.8	6.8	37.4	12.9	65.1	75.5	73.0
32.5	1.6	48.6	29.8	33.2	1.7	34.7	25.8	33.1	1.4	34.3	24.8	31.2	1.7	33.7	25.0	63.8	67.6	14.3
33.3	2.0	66.0	22.3	33.5	2.1	35.6	24.8	33.8	2.0	36.4	24.4	32.8	1.9	35.8	23.8	77.0	80.8	40.3
33.1	1.8	59.0	23.5	33.3	1.6	36.1	26.4	33.8	1.8	36.5	25.5	32.2	2.0	35.5	25.8	56.6	83.6	36.8
32.4	1.6	44.5	36.2	32.1	1.5	34.6	26.8	33.8	1.5	36.2	27.4	31.4	1.9	34.8	25.0	33.3	85.0	15.3
33.6	2.5	66.9	9.0	33.3	2.3	35.1	22.0	33.9	2.5	36.3	23.2	33.6	2.7	35.8	21.6	56.5	72.8	71.5