Temporal and spatial differences in three-egg clutch frequency of the
African Black Oystercatcher§

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African Black Oystercatchers *Haematopus moquini* produce a modal clutch size of two eggs and only rarely lay three eggs. A review of over 4 000 nest records from across their breeding range (dating back to the early 1960s) revealed that three-egg clutches have become more frequent, rising from 2% of recorded clutches before 1975 to >5% since 2000. Three-egg clutches are found predominantly in the south-western Cape and are clustered at specific sites in the region. They are produced earlier in the season compared to smaller clutch sizes and rarely occur after January. As this increase in three-egg clutch frequency is site specific, it might result from either a phenotypically plastic response to local resource availability, or a localised change in breeding system potentially resulting in more than one female laying in the same nest. While increased food availability might be the cause of changes in three-egg clutch frequencies, this is unlikely linked to the spread of the invasive mussel *Mytilus galloprovincialis*. Further research is needed to identify the cause of this phenomenon and evaluate how this change may affect the breeding success of this species.

**Keywords:** African Black Oystercatcher, avian reproduction, clutch size, geographic variation, *Haematopus moquini*

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**Introduction**

Clutch size (number of eggs per nest) varies within most bird species, driven predominantly by resource availability during egg-laying and chick-rearing (Skutch 1985; Martin et al. 2000). This is especially true for indeterminate layers (such as Anseriformes), which produce replacements for any egg losses sustained during laying (Kennedy 1991). In contrast, clutch sizes of determinate layers (e.g. many Charadriiformes; Kennedy 1991) are predetermined and show limited clutch size flexibility with environmental fluctuations.

Similar to other Charadriiformes, most oystercatchers (*Haematopodidae*) are determinate layers (Kennedy 1991) and produce clutches of one to four eggs (Hockey 1996). Small clutch sizes are strongly selected for because their chicks are precocial, and require feeding and protection throughout the fledging period (Safriel 1975). African Black Oystercatchers *Haematopus moquini* are monogamous (Hockey 1996; Kilner 2006) and lay a modal clutch of two eggs (Summers and Cooper 1977; Hockey 1985). Three-egg clutches are rare; the first three-egg clutch was recorded in Knysna in 1924 (Carlisle 1929). Hall (1959) found no three-egg clutches (*n* = 13) at Cape Point during 1958/59, and only one was found at the west coast islands from 1971 to 1980 (*n* = 138) (Summers and Cooper 1977; Hockey 1983). An increased frequency of three-egg clutches was noted over a 20-year study (1978–2002) of 733 clutches in the southern Cape (Jeffery and Scott 2005; Scott 2007) and more recently almost 4% (10 of 278) of clutches comprised three eggs on Robben Island during 2001–2005 (Braby and Underhill 2008; Tjørve and Underhill 2008). Since 1999, three four-egg clutches have been recorded for the first time (Oystercatcher Conservation Programme unpublished data).

Such an increase in clutch size is unusual in a determinate layer such as an oystercatcher and may have implications for their demography. These changes in clutch size have succeeded population increases over the last few decades (Loewenthal et al. 2015a), which were likely due to stringent protection laws, increased breeding success (Tjørve and Underhill 2006), and increasing food stocks resulting from the invasion of *Mytilus galloprovincialis* (Loewenthal et al. 2015a). Since the African Black Oystercatcher is an extensively studied species (over 50 years of monitoring records), we can attempt to understand whether an increase in three-egg clutches has occurred, even after increased observer effort is taken into consideration.

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account, and discover in which areas it is most prominent. We use historical African Black Oystercatcher nest records to identify possible temporal and spatial increases in three-egg clutches. Furthermore, we test whether this increase coincides with the invasion of *Mytilus gallo-provincialis*. If it does, this would be consistent with the hypothesis that the increase has occurred in response to an increase in food stocks.

**Methods**

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, with most breeding pairs found along the west coast (Summers and Cooper 1977; Loewenthal et al. 2015a) (Figure 1). They nest on the shore, feeding in the intertidal zone on mussels, limpets (Kohler et al. 2009) and polychaetes (Hockey 1984).

The African Black Oystercatcher has been well studied due to its Near Threatened status and charismatic appeal. This has resulted in over 4 000 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 h intervals) and containing nest location, sighting dates and clutch size were analysed to assess trends in clutch size. Multiple visits were needed to confirm maximum clutch size had been attained (i.e. clutch size remained constant for two successive visits).

**Variation in clutch size**

Nest records were sorted according to the coastal regions (defined by Hockey 1983) and adapted in Loewenthal et al. (2015b): Namibian Coast, West Coast, Lamberts Bay to Cape Point, Cape Point to Breede River, Breede River to Cape St Francis, and the East Coast (Figure 1). Temporal differences in clutch size were calculated by correlating both the average clutch size and percentage of three-egg clutches against year (1975–2014) as a continuous variable using a linear regression. The proportions of three-egg clutches for each decade during 1975 to 2014 were compared for the entire breeding range as well as for the separate coastal regions using chi-square tests. The clutch size of oystercatcher species can vary geographically (Väisänen 1977; Nol et al. 1984), so to identify whether geographic (latitudinal and longitudinal) correlations in clutch size occur, quarter-degree grid cells where nests were located were used to assign geographic coordinates. A generalised linear mixed model (GLMM; R package glmmML v. 1.0) was performed with nest site as a random effect to create binomial models determining the three-egg clutch probability as a function of latitude, longitude and year (one/two- to three-egg clutches). Nest site was a random factor in the GLMM because breeding pairs are faithful to the same location each year, and by adding it as a random factor it was possible to calculate the correlation of clutch sizes independent of site. Year was included in the model to remove the possibility that certain latitudes and longitudes might have inconsistent sampling. Models exhibiting the lowest AIC value are presented in the results.

African Black Oystercatchers breed during summer (November to March) with a peak in nest frequency in January (Summers and Cooper 1977; Tjørve and Underhill 2008). Only complete nest monitoring records (regular breeding site visits by the same observer from the start to the end of the breeding season) were used to establish when the seasonal peak of three-egg clutches occurred. This ensured that the results were not skewed towards favoured sampling months. Because the data set rarely included both measurements and mass for the same egg (which can be used to infer incubation stage and hence estimate laying date), lay dates were estimated by establishing the midpoint between initial nest sighting date and the previous visit, since sites were visited regularly (less than every 7 d). This can be obtained with accuracy because African Black Oystercatchers are territorial and pairs protect a single nesting territory year round (Hockey 1982; Loewenthal et al. 2015b, 2015c), which can be identified prior to nesting by the nest scrapes produced before laying commences.

Because nest threats are high 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), clutches are commonly replaced if the initial clutch is unsuccessful (Hockey 1982). These repeat clutches were also included in the seasonal comparison. Seasonal trends were analysed

![Figure 1: African Black Oystercatcher population and breeding range across southern Africa, showing (a) coastal regions where nest records where located and (b) high-intensity monitoring sites. Circles indicate the number of nest records per breeding zone.](image-url)
by comparing the total percentage of three-egg clutches and one/two-egg clutches occurring within each month (October–April) of the breeding season. A generalised linear model (GLM; binomial) was then performed to calculate the effect of season (Julian day) on three-egg clutch probability (one/two [0] to three-egg [1] clutches). Due to their scarcity four-egg clutches were not included in any of the analyses.

**Influence of *Mytilus galloprovincialis***

The introduction and spread of the invasive Mediterranean Mussel *Mytilus galloprovincialis* has been suggested to be a factor influencing the frequency of three-egg clutches (Loewenthal 2007) because this species was first noted on the west coast in 1985, around the time three-egg clutch frequency initially increased. Since then it has spread into southern Namibia (Hockey and van Erkom Schurink 1992; Branch and Steffani 2004), and was intentionally introduced to Port Elizabeth in 1990 (Branch and Steffani 2004). *Mytilus galloprovincialis* has altered the rocky shore species composition and now comprises a large percentage of the total rocky shore biomass (Hockey and van Erkom Schurink 1992). *Mytilus galloprovincialis* has replaced many of the oystercatchers’ native food sources (Branch and Steffani 2004) and may have had an influence on the frequency of three-egg clutches. We tested whether the increase in three-egg clutches coincided with the years in which *M. galloprovincialis* invaded each section of coastline (Figure 1). The invasion dates for many of the sites are known, and we interpolated dates for unknown sites assuming constant invasion rates between localities of known invasion year (Loewenthal et al. 2015a). It is likely that mussel density or biomass would not increase evenly across all the sites, thus creating a lag in establishment dates of ±5 years (Branch and Steffani 2004).

**Results**

**Temporal and spatial variation in clutch size**

African Black Oystercatchers showed a significant increase in the proportion of total clutches being three-egg clutches both when proportion of three-egg clutches were regressed against year as a continuous variable ($R^2 = 0.2357$, $F_{3,84} = 12.64$, $p < 0.001$), and when the proportion of three-egg clutches were compared between the four decades ($\chi^2 = 9.37$, $p < 0.05$) (Figure 2). A similar correlation was not found for the average clutch size, however, since a significant increase was not noted over these years ($R^2 = 0.0002$, $F_{3,84} = 1.788$, $p > 0.1$).

Similar to their congeneric species (Väisänen 1977; Nol et al. 1984), correlations between clutch size and latitude do occur resulting in a higher prevalence of three-egg clutches as latitude increases (Table 1). This is confirmed by the increase in three-egg clutch frequency occurring mainly from Lamberts Bay to Cape Point ($\chi^2 = 7.48$, $p < 0.01$), Cape Point to Breede River ($\chi^2 = 51.48$, $p < 0.001$), and Breede River to Cape St Francis ($\chi^2 = 4.44$, $p < 0.05$) (Figure 2). Contrary to this trend, the high-density island sites along this range (Malgas and Jutten Island, $n = 80$ clutches) have produced few, if any, three-egg clutches with only low-density island sites such as Dassen Island showing an increase in three-egg clutch frequency (14 three-egg clutches out of 415 clutches). Namibia and the west coast produced no three-egg clutches and the east coast maintained a constant frequency (4%) of three-egg clutches over the past four decades (Figure 2).

**Seasonal variation in clutch size**

The earliest recorded laying date was 10 October. Contrary to other findings, nesting attempts (clutches laid) peaked in December. Unlike one- and two-egg clutches, which peaked in December and January, three-egg clutches ($n = 47$) tended to occur earlier in the season with most being laid in November and December (Figure 3). No three-egg clutches were recorded after February. Further analysis validated season (days after start of season [Julian day]) as a significant parameter, predicting a negative relationship between three-egg clutch probability (one/two [0] to three-egg [1] clutches) and date (GLM binomial, estimate $= -0.018 \pm 0.005$, $t = -3.209$, $p = 0.001$).

**Invasion effects on clutch size**

There was no obvious correlation between the invasion date of *M. galloprovincialis* and the increase in three-egg clutch frequency (Figure 2, Table 2). If a potential lag effect of five years is added to the *M. galloprovincialis* invasion dates (to allow for establishment) the only coastal area to correlate is between the Breede River and Cape St Francis. In addition, there were no increases in three-egg clutch frequency associated with the spread of invasive mussels on the Namibian coast.

![Figure 2: African Black Oystercatcher average three-egg frequency (% across six coastal regions of southern Africa over the last four decades](image)

**Table 1:** Parameter estimates and likelihood ratio tests of the GLMM for African Black Oystercatcher three-egg clutch probability (one/two [0] to three-egg [1] clutches) as a function of latitude, longitude and year. The random effect for the GLMM was Site

| Parameter   | Value   | SE       | df | t-value | p-value |
|-------------|---------|----------|----|---------|---------|
| (Intercept) | -72.797 | 25.372   | 2503 | -2.869  | 0.004   |
| Latitude    | 0.347   | 0.189    | 2503 | 1.836   | 0.067   |
| Longitude   | 0.055   | 0.044    | 2503 | -1.237  | 0.216   |
| Year        | 0.0290  | 0.012    | 2503 | 2.376   | 0.018   |
Discussion

This study confirmed that there has been an increase in three-egg clutch frequency across the southern part of the range of African Black Oystercatchers. It is not clear what causal factors influence intraspecific clutch size variation within determinate layers such as Charadriiformes (waders), 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 van Treuren 1998; Totterman and Harrison 2007; Craik 2010) have been focal points in previous research. In light of the results of this paper we further discuss the spatially restricted causal factors that may account for the localised increase in three-egg clutch frequency.

The increased frequency of three-egg clutches from 2% pre-1975 to over 5% is a notable change for the African Black Oystercatcher, and although the increase of three-egg clutches does not alter the modal clutch size, this may still have implications for future populations. As the increase in three-egg clutch frequency is currently focused in the Western Cape, it is likely linked to changes occurring primarily in this region. Monogamous pairs may be laying three-egg clutches as a result of favourable conditions (presumably through phenotypic plasticity), such as an increase in resource availability, which lowers the costs of egg-laying and chick-rearing, or decreased predation risk, which increases the reproductive value of a given clutch (Lima 1987; Martin et al. 2000; Zanette et al. 2011). However, as three-egg clutches do not occur at the high-density island sites, the likelihood of predation pressure being an important factor is minimal since the predation rate at these sites is very low (Hockey 1982). Therefore, three-egg clutches are more likely resource-driven rather than predation-driven because pairs breeding at high-density island sites experience more competition but less predation.

Given that most three-egg clutches appear within the first three months of the breeding season, this may suggest increased investment early on, since reproductive success at this time might be maximised as a result of reduced competition (Verhulst and Nilsson 2008), and females of higher quality may be able both to breed earlier and to lay three-egg clutches. The timing of egg laying within the season is important for many species because the success of the first-laid clutch can be greater than subsequent clutches (Verhulst and Nilsson 2008). The subsequent reduction in the larger clutch sizes (three-eggs) noted in this study as the season progressed is also found with other waders (Väisänen 1977; Nol et al. 1984; L’Hyver and Miller 1991), and may be linked to a reduction in female physical condition after each lay (Moreau 1944a; Nol et al. 1984), or that pairs laying their first clutch later in the season are probably inexperienced individuals and poorer quality (van de Pol et al. 2006). If resources for chick-rearing allow, fledgling output should increase for pairs producing three-egg clutches and thus influence the overall population.

As the availability of food resources (during both breeding and non-breeding seasons) have been identified as an important factor in determining the clutch size of waders (Moreau 1944a), it is likely that anthropogenic changes to the rocky shore biomass (as a result of alien invasions and human collections) may have a major impact. Other determinate layers, such as the Tengmalm’s Owl Aegolius funereus (Hörnfelt and Eklund 1990, Korpimäki and Hakkarainen 1991) also show similar increases in clutch size when spikes in prey occur. However, they more commonly show a reduction in clutch size when resources are scarce (Korpimäki and Hakkarainen 1991). This arises because the ability to acquire food, particularly in temperate, resource-limited areas, reduces overall clutch

Table 2: Estimated invasion dates of Mytilus galloprovincialis and recorded decade of increased frequency of three-egg clutches, for each defined coastline within the study. Date of establishment (±5 years)

| Coastline                  | Date introduced | Decade of three-egg clutch increase |
|----------------------------|-----------------|-----------------------------------|
| Namibian Coast             | 1986 to 1994    | no increase                       |
| West Coast                 | 1981 to 1984    | no increase                       |
| Lamberts Bay to Cape Point | 1979 to 1983    | 1995 to 2004                      |
| Cape Point To Breede River | 1983 to 1989    | 1995 to 2004                      |
| Breede River to Cape St Francis | 1989 to 1994 | 1995 to 2004                      |
| East Coast                 | 1991 to 2000    | no increase                       |

Figure 3: Percentage of (a) one- and two-egg clutches (n = 1 442) and (b) three-egg clutches (n = 47) occurring monthly through the African Black Oystercatcher breeding season (re-lays included)
size (Skutch 1985; Martin et al. 2000), and limits the proportion of pairs able to breed (Skutch 1985; Martin et al. 2000). In areas where resources are more abundant, bird density and range size (Figueroa and Green 2006) have a greater effect on clutch size than food availability alone (Skutch 1985; Martin et al. 2000). This may imply that clutch size in high-density areas is naturally restricted by competition for resources, and may be the case at high-density island populations where few, if any, three-egg clutches occur.

This resource-driven response is supported by 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). The observed latitudinal correlation between three-egg clutch frequency has also been recorded in the Red Phalarope (Phalaropus fulicarius) (Schamel and Tracy 1987), European Oystercatcher (Haematopus ostralegus) (Väisänen 1977) and American Oystercatcher (Haematopus palliatus) (Nol et al. 1984). Up until now, no such patterns have been found in the African Black Oystercatcher (Summers and Cooper 1977) and other range-restricted species such as the American Black Oystercatcher (Haematopus bachmani) (L’Hyver and Miller 1991). This correlation is primarily due to the improved resource availability as one moves away from the equator.

Although the invasion of M. galloprovincialis does appear to benefit the oystercatcher population due to an increase in food availability (Loewenthal et al. 2015a), it is unlikely to be the primary contributing factor to the increased frequency of three-egg clutches, since the increase in three-egg clutches does not appear to coincide with most of the introduction dates of M. galloprovincialis. Although these dates of invasion do not necessarily translate into uniformly increasing M. galloprovincialis density or biomass due to varying coast type and exposure (Branch and Steffani 2004), the fact that many of the sites now containing M. galloprovincialis have had little or no increase in three-egg clutch frequency means that they cannot be the only influencing factor. In addition, 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 rocky shore biomass (Branch and Steffani 2004) and oystercatcher diet. Although M. galloprovincialis is a less preferred food source than limpets given its lower energy content (Coleman and Hockley 2008), the invasion has still necessitated reliance by African Black Oystercatchers on the mussel as a food source (Coleman and Hockley 2008). Male African Black Oystercatchers previously fed on limpets and females on bivalves to reduce intraspecific competition (Hockey and Underhill 1984; Kohler et al. 2009), but since the invasion both feed equally on M. galloprovincialis (Hockey et al. 2003; Coleman and Hockey 2008). The potential relationship between M. galloprovincialis and three-egg clutches is further contradicted by the fact that M. galloprovincialis was not established at De Hoop (Loewenthal et al. 2015a) when three-egg clutches were noted as increasing in frequency (Scott 2007), and breeding pairs in Port Elizabeth have not shown any change in three-egg clutch frequencies since the introduction and spread of M. galloprovincialis in 1990. Although there is no strong correlation between the invasion of M. galloprovincialis and three-egg clutches, improved resources are still a likely factor as anthropogenic effects are changing the biomass of most of the sites producing the three-egg clutches (DMP et al. unpublished data).

Cooperative polygyny is likely to produce a similar localised increase in clutch sizes as a result of males mating 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 is known to result in larger than modal clutch sizes amongst the European Oystercatcher, which can produce clutches of up to six eggs (Heg and van Treuren 1998), and the Australian Pied Oystercatcher Haematopus longirostris, which produce a clutch size of up to four eggs (Totterman and Harrison 2007). In the African Black Oystercatcher, however, there is little evidence of a change in breeding strategy (Paijmans et al. in prep) and this theory is only supported by anecdotal evidence of a third adult accompanying a pair at Cape Recife (Philip Whittington and Anthony Tree, pers. comm.).

Conclusion

The increase in three-egg clutch frequency temporarily represents a significant change in the breeding pattern of African Black Oystercatchers. Because the increase is site specific it is likely due to either an increase in pairs laying three-egg clutches as a result of favourable conditions (phenotypic plasticity or even microevolution) or a localised change in breeding strategy (polygyny or egg dumping). Further work is needed (especially on sites with little or no change to the three-egg clutch frequency) to identify which of these phenomena are occurring and to determine the driving factors behind them in an attempt to understand the future impacts for this species and to understand the dynamics of the clutch sizes of determinate layers as a whole.

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