African Penguins *Spheniscus demersus*, bait balls and the Allee effect

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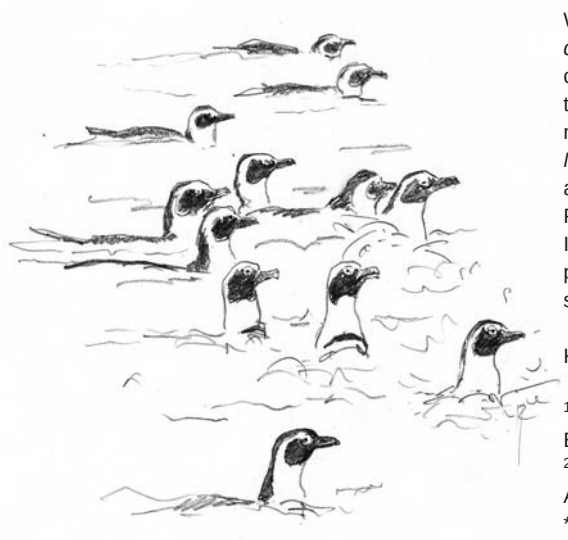

We report co-operative group foraging in the African Penguin *Spheniscus demersus*. Groups of approximately 25–165 African Penguins were observed circling schools of pelagic fish, sometimes forcing them to the surface. During this behaviour 66–75% of penguins were underwater at any given time. Smaller numbers of African Penguins also joined foraging groups of Cape Gannets *Morus capensis* and Cape Cormorants *Phalacrocorax capensis*, but did not appear to corral fish schools when outnumbered by these species. African Penguins are listed as Endangered due to ongoing rapid population decreases. If group foraging confers an advantage to African Penguins, their dwindling populations may suffer from an Allee effect as colonies become too small to support sufficient densities of birds for foraging groups to form.

Key words: group foraging, Benguela, anchovy, sardine, predation

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The population of African Penguins *Spheniscus demersus* has fallen dramatically over the last decade (Crawford *et al.* 2011) and the species recently has been uplisted from Vulnerable to Endangered (BirdLife International 2010). The most plausible explanation for the recent collapse is a decrease in the availability of small pelagic fish, their preferred prey, particularly in the vicinity of breeding colonies (Pichegru *et al.* 2010, Crawford *et al.* 2011). Despite numerous investigations of their foraging ecology (e.g. Wilson 1985, Wilson & Wilson 1995, Petersen *et al.* 2006, Ryan *et al.* 2007), little is known about how African Penguins locate and capture their prey (although they may use scent to select productive areas at a coarse spatial scale; Wright *et al.* 2011). Based on the position of bite marks on fish (Wilson & Duffy 1986) and observations of groups of penguins circling schools of pelagic fish (Wilson *et al.* 1987), Rory Wilson inferred that at least some African Penguin foraging is cooperative, herding preferred prey into dense schools, then striking from below. Their conspicuously striped adult plumage appears to promote dense, defensive schooling of small pelagic fish, creating so-called 'bait balls' that are easier to exploit (Wilson *et al.* 1987). However, it is unclear how often this behaviour occurs, or how large a group is required to corral a school of fish effectively.

Cooperative hunting is one of the classic mechanisms underpinning an Allee effect, whereby the growth rate of a small population decreases with population size (inverse density dependence; Courchamp *et al.* 1999). Simplistically, as a population's size dwindles, there are too few individuals to allow effective cooperative hunting. This effect has not been explored in African Penguins, largely because of the paucity of empirical data on their cooperative foraging behaviour. Wilson *et al.* (1986) argued that African Penguins do not forage in groups of more than 20 birds, because they cannot synchronise their diving. However, we present observations of several hundred African Penguins foraging together, suggesting that Allee effects linked to cooperative hunting may be an issue in larger populations than previously thought.

Methods

African Penguins breed at two island groups in Nelson Mandela Bay, Eastern Cape South Africa: St Croix and Bird Islands. Together, these islands currently support more than a third of all African Penguins, with St Croix being home to the largest single colony (Crawford *et al.* 2011). Raggy Charters has been running small boat tours to view marine mammals and seabirds in Nelson Mandela Bay since 2002. Foraging groups of seabirds often are investigated during these tours, and some of these aggregations have been photographed by LE. We searched this photographic archive for groups containing African Penguins. Multiple images were available for each foraging group. We identified the birds and counted the numbers of each species in each image. The maximum count for each species was taken as a minimum estimate of numbers of birds in a given foraging group. We could also estimate the minimum duration of a foraging event, although most groups are only spotted after they form, and it was not always possible to remain with a foraging group for the duration of the foraging event. Spearman rank correlations were used to test for relationships between group size and duration. In some instances there were images of the foraging group after foraging ceased, when most penguins were resting on the surface. By comparing the number of birds present in these images we estimated the proportion of birds on the surface compared to those underwater when foraging. Similar correction factors could not be obtained for cormorants or gannets, as some depart the area before foraging ceases.

Results

Thirteen foraging groups involving African Penguins were photographed (n = 95 images) from 2003 to 2010, mainly in summer (October–March), outside the African Penguin's peak breeding period. Water clarity was reasonably good on most occasions, but sampling was not random because the small boat tours only run during relatively calm conditions. Eight aggregations involved penguins swimming in a clearly defined circle 3–10 m in diameter (Figure 1A). That the penguins were circling small pelagic fish was evident in at least two cases, because a dense school of fish (presumably Anchovy *Engraulis capensis*) was brought to the surface (Figure 1B). Penguins were the dominant species in all these foraging groups, but they often attracted large numbers of terns, especially Common Terns *Sterna hirundo* (Table 1), which were able to exploit the fish by surface dipping. Penguin orientation on surfacing was random in the other five foraging groups, suggesting that they were not co-ordinating their foraging effort. These groups contained larger numbers of Cape Gannets *Morus capensis* (n = 3, 15–25 individuals) or Cape Cormorants *Phalacrocorax capensis* (n = 2, 25–50 individuals), which may have prevented the African Penguins from forming a tight, circling group. Fewer African Penguins attended these foraging aggregations than those where circling behaviour was observed (Table 1). Gulls attended both types of aggregations. Kelp Gulls *Larus dominicanus* were more abundant at mixed-species aggregations whereas Grey-headed Gulls *Chroicocephalus cirrocephalus* were more frequent at penguin-dominated feeding groups (Table 1), although this may have been influenced by the location of foraging groups, as Grey-headed Gulls tend to remain close to shore.

Numbers of penguins, cormorants and gannets reported in Table 1 are minimum estimates, because some individuals were underwater when the photographs were taken. In four instances a group was followed until foraging ceased, whereupon most if not all penguins rested on the water surface. In all four cases the maximum number of penguins counted on the surface was 3–4 times (average 3.5 ± 0.5) that when they were foraging (Figure 2). This implies that the average group size of penguins feeding in penguin-dominated groups is around 150 individuals, compared to an average of only 45 penguins in mixed-species aggregations. The smallest circling group of penguins photographed had 8 birds on the surface, suggesting that 25–30 birds are required to corral a school of fish.

Table 1. Minimum numbers of birds in foraging groups containing African Penguins in Nelson Mandela Bay, Eastern Cape, South Africa. Two types of groups were recorded: those where penguins surfaced in a coherent direction, apparently circling their prey, and those where orientation on surfacing was random.

Species	Penguins circle prey (n = 8)	Random orientation (n = 5)
	Mean ± SD (range)	Mean ± SD (range)
African Penguin[a]	43.6 ± 33.3 (8–92)	13.0 ± 9.7 (3–26)
Cape Gannet	0.3 ± 0.7 (0–2)	12.0 ± 11.5 (0–25)
Cape Cormorant	3.8 ± 4.1 (1–10)	18.4 ± 20.4 (0–50)
Kelp Gull	3.6 ± 4.3 (0–10)	23.8 ± 20.8 (1–50)
Grey-headed Gull	1.3 ± 3.5 (0–10)	0.2 ± 0.4 (0–1)
Terns[b]	39.8 ± 44.6 (0–105)	20.4 ± 24.0 (0–60)
All birds	92.4 ± 44.4 (23–138)	87.8 ± 37.0 (50–137)

[a] Excludes post-foraging counts of some groups which indicate the total number of penguins is 3–4 times greater than the number at the surface during foraging.
[b] 89% Common Terns *Sterna hirundo*, 11% Swift Terns *Thalasseus bergii*, and <1% Sandwich Terns *T. sandvicensis*.

Figure 1. An African Penguin feeding group showing a clear clockwise circling pattern (top) and a smaller group (bottom) that has driven a bait ball of small fish right to the surface (visible as a silver mass in the centre of the picture). Photos by Lloyd Edwards.

Figure 2. African Penguins circling a school of fish (top) and 2 min later (bottom) after foraging activity ceased, showing roughly three times as many birds resting on the surface (at least 158) than visible while foraging (*c.* 50). Photos by Lloyd Edwards.

Foraging events lasted at least 5.4 ± 4.6 min, with no difference between penguin-dominated groups (5.7 min, range 2–14 min) and mixed-species groups (5.0 min, range 1–12 min). There was no relationship between penguin group size and foraging duration ($r_s = 0.512$, $n = 11$, $P > 0.1$) but larger groups foraged for longer when all species were combined ($r_s = 0.618$, $n = 11$, $P = 0.05$).

Discussion

The number of foraging groups photographed is rather small, and there may be a bias towards larger groups because they are more conspicuous. However, it is clear that African Penguins forage in larger groups than reported previously (Wilson *et al.* 1986) and that synchronised diving is not a prerequisite for group foraging (*contra* Wilson *et al.* 1986) as 25–33% of penguins are on the surface at any time during these foraging events. Species composition of the foraging groups appears to influence penguin behaviour, with penguins circling fish schools when they are the dominant deep-diving species, but seemingly not doing so when there are large numbers of other diving species (Cape Gannets and Cape Cormorants). It is plausible that the presence of large numbers of other diving birds disrupts the penguins' ability to effectively corral a fish school; underwater observations are required to confirm this speculation. A similar situation was witnessed at the Snares Islands, New Zealand, where Sooty Shearwaters *Puffinus griseus* displaced Antarctic Terns *Sterna vittata* from crustacean swarms through physical interference (Sagar & Sagar 1989).

Our observations show that African Penguins forage in large groups at least occasionally, despite their current small population size. It must be increasingly difficult to form such groups as colony sizes decrease (Crawford *et al.* 2001, 2011) and their foraging ranges while breeding increase (Pichegru *et al.* 2010). Acting in concert, these two factors greatly reduce the density of penguins at sea around breeding islands. Whether a decrease in group foraging behaviour results in an Allee effect depends on whether it is more profitable to forage in large groups than singly or in small groups. Although such data currently are unavailable for African Penguins, it seems plausible that group foraging does enhance the rate of prey capture. Many seabirds are primarily group foragers, and their individual foraging success improves with increasing group size (Götmark *et al.* 1986). By working together, seabirds targetting fish schools benefit by disrupting the cohesiveness of predator avoidance tactics (Shealer 2002; see also Wilson *et al.* 1987).

If large group foraging is more rewarding for African Penguins, the strength of the Allee effect will be related in part to the frequency with which such foraging occurs. Observations at sea off the Western Cape of South Africa in the 1980s suggest that most penguins forage singly or in small groups (<5 birds; Wilson *et al.* 1988). Whether this has changed as the population of African Penguins has decreased is uncertain. The earliest observations of penguin group sizes at sea occurred in the 1950s, when the population had already decreased substantially, and there was no decrease in the size of penguin groups at sea between 1954–74 and the 1980s, despite the regional population of African Penguins more than halving over this period (Wilson *et al.* 1988). Current data on penguin group sizes at sea would be useful to compare with previous estimates. At face value, the fact that group size at sea remained unchanged from the 1950s to the 1980s suggests that group foraging is not very important for African Penguins. However, penguin-mounted cameras revealed that Chinstrap Penguins *Pygoscelis antarctica* forage in groups more often than previously thought (Takashi *et al.* 2004). It should be feasible to infer the importance of penguin-dominated group foraging by equipping African Penguins with dead reckoning loggers to detect how often they undertake circling activity. However, it is inevitable that foraging in large groups will become increasingly difficult for birds in very small colonies (<50 pairs), potentially increasing their risk of local extinction (Crawford *et al.* 2001).

References

BirdLife International 2010. Threatened birds of the world. www.birdlife.org.

Courchamp F., Clutton-Brock T. & Grenfell B. 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. 14: 405–410.

Crawford R.J.M., David J.H.M., Shannon L.J., Kemper J., Klages N.T.W., Roux J.-P., Underhill L.G., Ward V.L., Williams A.J. & Wolfaardt A.C. 2001. African penguins as predators and prey – coping (or not) with change. Afr. J. Mar. Sci. 23: 435–447.

Crawford R.J.M., Altwegg R., Barham B.J., Barham P.J., Durant J.M., Dyer B.M., Makhado A.B., Pichegru L., Ryan P.G., Underhill L.G., Upfold L., Visagie J., Waller L.J. & Whittington P.A. 2011. Collapse of South Africa's penguins in the early 21st century: a consideration of food availability. Afr. J. Mar. Sci. 33: 139–156.

Götmark F., Winkler D.W. & Andersson M. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature 319: 589–591.

Petersen S.L., Ryan P.G. & Grémillet D. 2006. Is food availability limiting African Penguins at Boulders Beach? A comparison of foraging ecology at mainland and island colonies. Ibis 148: 14–26.

Pichegru L., Grémillet D., Crawford R.J.M., & Ryan P.G. 2010. Marine no-take zone rapidly benefits threatened penguin. Biol. Letters 6: 498–501.

Ryan P.G., Petersen S.L., Simeone A. & Grémillet D. 2007. Diving behaviour of African Penguins: do they differ from other *Spheniscus* penguins? Afr. J. Mar. Sci. 29: 153–160.

Sagar P.M. & Sagar J.L. 1989. The effects of wind and sea on the feeding of Antarctic Terns at the Snares Islands, New Zealand. Notornis 36: 171–182.

Shealer D.A. 2002. Foraging behavior and food of seabirds. In Schreiber E.A. & Burger J. (eds) Biology of Marine Birds. CRC Press, Boca Raton, pp. 217–262.

Takashi A., Sato K., Naito Y., Dunn M.J., Trathan P.N. & Croxall J.P. 2004. Penguin-mounted cameras glimpse underwater group behaviour. Proc. R. Soc. Lond. B 271: S281–S282.

Wilson R.P. 1985. The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. Mar. Ecol. Progr. Ser. 25: 219–227.

Wilson R.P. & Duffy D.C. 1986. Prey seizing in African Penguins *Spheniscus demersus*. Ardea 74: 211–214.

Wilson R.P. & Wilson M-P.T. 1995. The foraging behaviour of the African Penguin *Spheniscus demersus*. In Dann P., Norman I. & Reilly P. (eds) The Penguins Surrey Beatty & Sons, Chipping Norton, pp. 244–265.

Wilson R.P., Wilson M-P.T. & McQuaid L. 1986. Group size in foraging African Penguins (*Spheniscus demersus*). Ethology 72: 338–341.

Wilson R.P., Ryan P.G., James A. & Wilson M.-P. 1987. Conspicuous coloration may enhance prey capture in some piscivores. Anim. Behav. 35: 1558–1560.

Wilson R.P., Wilson M-P.T. & Duffy D.C. 1988. Contemporary and historical patterns of African Penguin *Spheniscus demersus*: distribution at sea. Estuar. Coast. Shelf Sci. 26: 447–458.

Wright K.L.B., Pichegru L. & Ryan P.G. 2011. Penguins are attracted to dimethyl sulphide at sea. J. Exp. Biol. 214: 2509–2511.

Samenvatting

Dit artikel beschrijft het foerageergedrag van Afrikaanse Pinguïns *Spheniscus demersus* voor de kust van Zuid-Afrika. Tijdens het onderzoek zocht de soort voedsel in groepen van 25–165 vogels, waarbij grote scholen vis ingesloten werden. De pinguïns verbleven dan lange tijd onder water: op enig moment waren niet meer dan 25–33% van de vogels aan het wateroppervlak zichtbaar. Ook sloten de pinguïns zich aan bij groepen voedselzoekende Kaapse Jan van Genten *Morus capensis* en Kaapse Aalscholvers *Phalacrocorax capensis*. De aantallen waren dan wel kleiner en de vogels dreven de visscholen niet op. De populatie van de Afrikaanse Pinguïn neemt snel in omvang af en heeft tegenwoordig de status van een bedreigde soort. Aannemende dat de pinguïns baat hebben bij groepsgewijs voedsel zoeken, dan zou de populatie te lijden kunnen krijgen van het zogeheten Allee-effect: het (foerageer)succes van individuen neemt af naarmate de populatie kleiner wordt. De dichtheid aan pinguïns is dan te laag om voldoende grote groepen tijdens het vissen te kunnen vormen. (JP)

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