Flock distributions of Lesser Flamingos *Phoeniconaias minor* as potential responses to food abundance-predation risk trade-offs at Kamfers Dam, South Africa

MARIA V.J. HENRIKSEN, SUSAN HANGSTRUP, FREDERIK WORK, METTE K. KROGSGAARD, GEOFFREY B. GROOM & ANTHONY D. FOX*

Department of Bioscience, Aarhus University, Kalø, Grenåvej 14, DK-8410 Rønde, Denmark.
*Correspondence author. E-mail: tfo@bios.au.dk

Abstract

Digitised vertical aerial photography was used to investigate the instantaneous distributional patterns of Lesser Flamingos *Phoeniconaias minor* at Kamfers Dam, South Africa. Image processing software was applied to differentiate high and low density flocks, based on earlier work, suggesting formation of dense aggregations in response to food abundance (in this case, the cyanobacteria *Arthrospira fusiformis*). Ripley's K analysis showed a regular arrangement of individuals in the densest flocks, potentially reducing interference without cost to foraging efficiency in highest food concentrations. Where inter-bird distances exceeded 0.70 m (s.d. ± 0.06 m, 95% C.I.), flamingos were arranged irregularly and showed clustered distributions. Flamingos aggregated to forage in the densest flocks in shallow waters, but imagery showed that the birds always maintained a consistent distance from mainland shorelines, whereas on an isolated artificial island they showed no such avoidance pattern. We hypothesised that this distance was maintained due to perceived predation risk from mainland predators and predicted that it would be inversely correlated with flock size (due to predator detection and dilution effects) but positively correlated with vegetation on shore (which functions as cover for predators). Generalised linear mixed modelling showed that flocks adjacent to vegetated shores (mean = 14.0 m ± 2.9, 95% C.I.) were arranged significantly further from the shore than those near unvegetated shorelines (4.1 m ± 2.8, 95% C.I.), supporting our second hypothesis. However, there was no correlation with flock size over the range of flock sizes included in the analysis, suggesting that flock size benefits are more related to foraging than to predation avoidance. We suggest that the density, shape and position of Lesser Flamingo flocks at this site is driven by food abundance but modified by

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perceived risk of predation. Further studies combining simultaneous aerial survey and mapping of food density and distribution are required to verify the precise relationships involved.

Key words: flocking behaviour, inter-bird distance, predation risk, spatial distribution, trade-off.

Animals select feeding patches which enable the highest energetic intake rate, while expending the minimum harvesting effort (MacArthur & Pianka 1966). In situations where food is super-abundant in three-dimensional space, predators can aggregate into and sustain very high foraging densities with minimal prey depletion effects, at least in the short term. For instance, Lesser Flamingos *Phoeniconaias minor*, filter feeding on diatoms and blue-green algae in the water column in which they stand, can reach densities of 5,400 individuals ha^{-1} (Tuite 2000). Filamentous blue-green algae are especially important dietary items of the Lesser Flamingo in Africa (Jenkin 1957); these algae and, to a lesser extent, diatoms can attain very high densities in African lakes as a food source for flocks of up to many thousands of Lesser Flamingos (Tuite 1979, 1981). This species frequently forms dense flocks in response to very high standing crops of blue-green algae, but when food biomass falls, the birds disperse to feed at far lower densities on the more predictable and widely dispersed diatoms (Tuite 2000).

Such aggregations of flamingo biomass (*e.g.* a mean of 0.755 kg m^{-2}; Tuite 2000), often in shallow water close to shore, also constitute a highly profitable feeding patch for the flamingos' predators. In East Africa, this include mammalian Side-striped Jackals *Canis adustus,* Golden Jackal *C. aureus,* Warthog *Phacochoerus africanus* (Moreno-Opo *et al.* 2013) and Spotted Hyenas *Crocuta crocuta*, as well as avian African Fish Eagles *Haliaeetus vocifer*, vultures (Accipitridae) and Marabou Storks *Leptoptilus crumeniferus* (Brown 1960; Nasirwa 2000). Foraging in dense flocks therefore may have a fitness cost due to the enhanced risk of predation, which in certain circumstances may need to be weighed against the benefits of foraging on an abundant food supply, especially where food is most abundant in shallow water and therefore in closest proximity to predators on land.

Evolutionary theory suggests that the main advantages of flocking are to increase foraging efficiency and reduce predation risk to the individual associated with such behaviour (Lima & Dill 1990). In the case of the Lesser Flamingo, both factors are likely to shape flocking behaviour, but how do these two drivers interact to affect flocking behaviour in this species in natural situations? In this study, historical vertical aerial photography of flocks of Lesser Flamingos obtained at Kamfers Dam, South Africa (Groom *et al.* 2011) are used to investigate, for the first time, how these birds distribute themselves in relation to flock density, aggregate in relation to food supply, and whether these distributions appear to be modified by the threat of

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predation (as per Lima & Dill 1990). As these images were obtained in 2006, we are now unable to gather contemporary prey data. Instead, use is made of the images of flamingo distribution to hypothesise about the patterns observed in them. Although this restricts the inferences that can be made from the data, it does provide support for theories that can be tested in the field in future studies.

Shifts in the phytoplankton community of soda lakes in the East African Rift Valley influence the distribution of Lesser Flamingos that aggregate in high densities in such water bodies (Brown 1959; Vareschi 1978; Harper *et al.* 2003; Krienitz & Kotut 2010). The super-abundant cyanobacterium *Arthrospira fusiformis* forms the main food source for these birds (Vareschi 1978; Owino *et al.* 2001) and studies at various sites have shown that Lesser Flamingo numbers were significantly positively correlated with *Arthrospira* biomass (*e.g.* Melack & Kilham 1974; Kaggwa *et al.* 2013; Kihwele *et al.* 2014). *Arthrospira fusiformis* is likewise the Lesser Flamingo's main food at Kamfers Dam (Anderson 2008; Hill *et al.* 2013). Given the absence of contemporary prey data we therefore make the assumption that the highest densities of feeding Lesser Flamingos recorded on the aerial photographs were gathered in response to *Arthrospira* distribution, and also that there is constant predation risk at the site, resulting in flamingo densities reaching their maxima in association with dense blooms of their blue-green algae prey. In such a situation, we hypothesised that the birds were so close-packed that they were constrained only by the proximity to their neighbours. In contrast, away from such high food abundance and dense uniform groups of birds, aggregations were irregular and clustered. We interpret very high-density flocks as being associated with rich feeding patches, interspersed with areas of no birds or lower densities associated with other poorer quality sources of food (as observed in flamingo flocks elsewhere: Bartholomew & Pennycuick 1973; Schmitz & Baldassarre 1992a; Tuite 2000). On considering inter-bird distances, we predicted an even (*i.e.* non-random) pattern of dispersal within flocks where there were very short distances between individuals, because birds maintain a regular "personal space" distance between themselves and their neighbours in tightly packed groups (Conder 1949; Schmitz & Baldassarre 1992a). Conversely, at lower densities, we anticipated that this regularity would break down and that at greater spatial scales the inter-bird distances would show a more clustered distribution reflecting the patchiness of the food supply.

We hypothesised that the risk of predation is not even across the habitat exploited by the flamingos. Although aerial predators (such as the African Fish Eagle, vultures and Marabou Storks) could theoretically strike anywhere on Kamfers Dam, the open nature of the majority of the habitat ensures that dense flocks of flamingos would be able to detect predatory birds over long distances. Where the shoreline is more broken by topography and tall, dense vegetation, predator detection rates are likely to be lower, although in dense flocks, the dilution effect still minimises the risk of an individual being eaten (Inman & Krebs 1987). Terrestrial and aerial predators

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mounting surprise predation attempts will, by necessity, attack their prey from the shore, most likely using some form of cover to conceal their approach. Much of the shoreline of Kamfers Dam is an open landscape comprising bare sand and mud flats, largely devoid of vegetation because of the annual fluctuations in water levels and the semi-arid nature of the climate. While these sections provide no concealment for potential predators, other sections of the shore are interrupted by rocky outcrops, dense scrub and forest, which do provide such cover. Flamingos in flocks generally maintain remarkably even distances between those flock members closest to land and the mainland shoreline (see Fig. 1). Because this is not the case on the artificial island situated more than 200 m from the nearest shoreline of the lake (Fig. 2), where there are no predators resident, we infer that flock avoidance of mainland shorelines is an anti-predation behavioural response. On this basis, we predicted that the distance between flocks and the shoreline would increase with increasing complexity of vegetation cover along the shore. Finally, if the benefits of combined vigilance and predation dilution to the individual from flocking were to have an effect, we predicted that larger flocks would approach closer to land with cover compared to smaller ones.

To summarise, we assumed that the high-density stratum of flamingo flocks corresponded to the highest prey density and preferred foraging depth. This reflected the optimum feeding distribution attainable with regard to both food availability (*i.e.* food accessibility and abundance) and safety from predators on the mainland. Considering only the densest flocks, we hypothesised that flamingos would trade-off feeding profitability with predation risk. From the hypotheses above, we therefore predicted that flamingos (i) in the densest parts of the flock would show regular inter-bird distances at small spatial scales, but show clustered distributions at greater spatial scales, (ii) would keep a threshold distance to the mainland shore to avoid predators, but that this distance would increase with the degree of vegetation cover

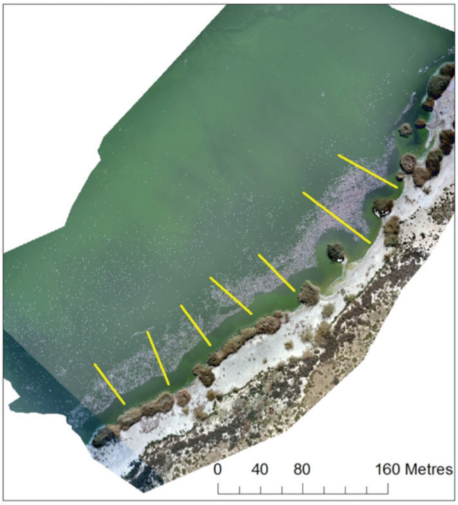

Figure 1. A typical vertical photographic image of one of the Lesser Flamingo flocks at Kamfers Dam, May 2006, showing consistent distances maintained by the nearest birds to the shoreline. Note also the ease with which it was possible to define the position of the shoreline at the time of the flight and to classify vegetation presence/absence (in this image as either partially or fully vegetated) in relation to the birds. Yellow lines indicate divisions made within continuous groups of Lesser Flamingos, to break flocks into smaller units for statistical analysis, as described in the text.

Figure 2. Vertical photographic image of the artificial island at Kamfers Dam, May 2006. Note that, in the absence of terrestrial predators, Lesser Flamingos occur all over the island and in adjacent shallow waters. Also, unlike along all mainland shores (see Figs. 1 and 4), there is no sign of the birds avoiding the shoreline.

that provided cover for potential predator approach, and (iii) would reduce the distance to shore with increased flock size, as the perceived risk of being predated is lower in larger-sized flocks than in smaller ones.

Methods

Study area

Kamfers Dam (28.67°S, 24.76°E) near Kimberley, Northern Cape, South Africa, holds the largest resident aggregation of Lesser Flamingos in South Africa (Anderson 1994; Zimmerman *et al.* 2011), supporting nearly 82,000 individuals in May 2006 (Groom *et al.* 2011). Flamingos rarely bred here in the past, because suitable predator-free habitat was lacking. An artificial breeding island was established in 2006, which sustained successful rearing of 9,000–12,000 young annually for a number of years (Anderson 2008). Adult flamingos obtain their cyanobacteria food by filtering prey-rich water through the lamellae in their bill, sometimes whilst wading and swimming, but generally they prefer to feed whilst standing in shallow water and thus aggregate into dense feeding flocks close to the shoreline (Bartholomew & Pennycuick 1973). Foraging close to land exposes them to attacks from avian raptors from the air and from terrestrial predators pursuing them through shallow waters (Moreno-Opo *et al.* 2013). Although knowledge of the full range of predators affecting flamingos at Kamfers Dam is incomplete, Black-backed Jackal *Canis mesomelas,* Warthogs, Brown Hyenas *Hyaena brunea* and stray feral dogs *Canis familiaris* are the primary recorded predators, while African Fish Eagle (which breed in trees 700 m from the lake) and vultures are also present and known to take flamingos at the site (T. Anderson, pers. comm.).

Aerial survey data

Vertical images were obtained of the entirety of Kamfers Dam in May 2006 during a full aerial survey carried out by Azure Aerial Photography (Pty) Ltd. The survey was flown at *c.* 1,550 m above sea level and *c.* 455 m above lake level along five SW–NE track lines, generating 31 Agfa film 23 cm × 23 cm negative transparencies. The transparancies were each digitally scanned (to .tif format) by Chamelion Scans to give 24-bit red–green–blue (RGB) digital image data, with pixels representing ground elements of *c.* 8 cm × 8 cm. Each of these images was geo-rectified and the set were mosaicked according to WGS_1984_UTM_Zone_34s, with the pixel size set to 10 cm × 10 cm (Groom *et al.* 2011). Polygon shape-files (.shp) representing the instantaneous occurrence of each individual flamingo throughout the lake had previously been produced from the image data (Groom *et al.* 2011). These shape data represented the primarily flamingo individual distribution data used in this study. Images from the breeding island were not included in the study because of the predator-free nature of this site. Although Greater Flamingos *Phoenicopterus roseus* occur on Kamfers Dam, no more than a few dozen were present at the time of the aerial photography, so contribute a trivial amount to the numbers of flamingos present (Groom *et al.* 2011; M. Anderson, pers. comm.).

Spatial representation of flamingo densities based on segmentation algorithms

Bartholomew & Pennycuick (1973) found that Lesser Flamingos in African Rift Valley Lakes tended to occur in two distinct densities which we equated to the "clustered" (*i.e.* where flamingo distribution is more clustered than random) and "dispersed" (more dispersed than random) flock densities of Tuite (2000), in response to differences in food supply (*i.e.* super-abundant algae *versus* less abundant diatoms; Bartholomew & Pennycuick 1973; Tuite 2000). Flamingo flocks in our study therefore were described according to variation in flamingo density across the site by using the object-based image analysis software Trimble eCognition v9.0 (Benz *et al.* 2004; Trimble 2014). A multistep process was used to create polygons, representing high-density flocks of flamingos, through the combined use of the polygon shape-files representing the individual flamingos and, as a raster basis for the processing, the geo-rectified 10 cm × 10 cm pixel images. Single pixel objects were created and those objects coincident with a flamingo-shape polygon were assigned to the class "flam" and all other objects were assigned as "unclassified". Some of the flamingo polygons exceeded a single pixel (*e.g.* a pair or a set of 4 pixels), so the additional excess pixels were assigned to "unclassified" such that each flamingo was represented as a single 1-pixel object. A flamingo spatial density was evaluated for every individual single pixel object by determining the numbers of "flam" objects (*i.e.* pixels representing flamingos) present within a radius of 20 pixels. As running this evaluation on every single pixel object is computationally intense, the "unclassified" objects (*i.e.* pixels not denoted as flamingos) were initially merged to 10 × 10 pixel objects, with those situated > 50 pixels away from any "flam" objects set to the class "ignore" (*i.e.* pixels excluded from the remainder of the classification process). The remaining "unclassified" objects were then re-segmented to single pixel objects for the per-object count. The per-object count of the number of "flam" objects within a distance of 20 pixels was converted to an image layer with each pixel's value denoting the count value. A spatial domain median filter with a 7 × 7 pixel kernel (Russ 2011) was then applied to the image to form a spatially smoothed representation of

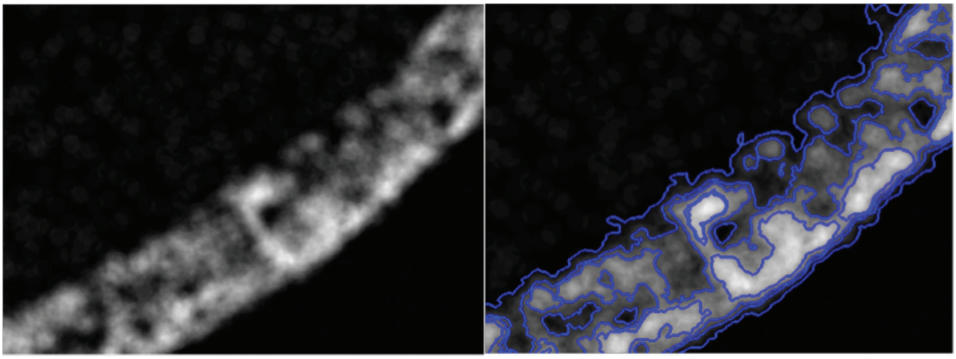

Figure 3. Depiction of a flamingo density raster computed using Trimble eCognition v9.0 (Benz *et al.* 2004; Trimble 2014). The lighter grey shades represent greater densities of flamingos. The right-hand figure depicts the raster separated into spatial units of different density ranges, identified by the blue contours.

flamingo density (Fig. 3). The image of flamingo densities was then simplified into spatial units of different density ranges using an image segmentation tool in eCognition. This tool transforms the set of single pixel objects into a smaller set of polygonal objects such that none of the resulting objects has an image pixel value standard deviation that was greater than a chosen threshold (Trimble 2014), which in this instance was set to 3.0. These objects were then exported as shape polygons, representing discrete flock units (Fig. 3), with their average density values set as attribute fields.

Distance between individuals

Flamingo point data derived as described above, within the dense flock polygon shape-files, were analysed using a Multi-Distance Spatial Cluster (MDSC) analysis in ArcGIS (ESRI 2013), based on Ripley's K-function which summarises the spatial dependence of point data across a range of distances (Ripley 1977). The analysis determines how the spatial clustering (more clumped than expected by chance) or dispersion (more regularly spaced than expected by chance over a given distance) of given point centres change with distance to neighbours (Dixon 2002) and, in this case, it portrays whether individual flamingos show dispersed or clustered patterns over increasing inter-object distances. The analysis was conducted using MDSC with the number of "Distance Bands" set to 100, "Beginning Distance" set to 0, "Distance Increment" set to 0.1, "Boundary Correction Method" set to simulate outer boundary values and the "Study Area Method" set to the corresponding shape-file for the investigated flock. Graphical output was obtained along with nearest neighbour distance data from each flamingo inside the designated area. By subjecting these data recorded from ArcGIS to the Ripley's K analysis, it was possible to identify graphically the distance at which the flamingos switched from being overly dispersed to overly clustered, which we interpreted to be the threshold distance kept between individuals. We here present the normalised Ripley's K function L(d), which simplifies comparisons with expectations of dispersed/clustering against a 1:1 norm (Besag 1977).

Distance to shore in relation to predator threat

The analysis gave rise to 15 discrete shape-files (one for each discrete flock), too few to facilitate a robust analysis of the effects of vegetation/topographical cover on the distance to shoreline. To generate more data points, the shape-files with a landward edge of > 50 m were split into sections of roughly 50 m length (see Fig. 1 for an example of this, and Fig. 4 for all other flock divisions used in the study). This increased sample size, encompassing extra varying degrees of shoreline vegetation and other cover associated with single flocks along their length. It resulted in 40 flock sub-units, which enhanced the power of our analysis when applying a linear mixed model to the data. Within each of the 40 sub-units, the individual closest to the shoreline (the waterline being defined on the shape-files directly from the images) was identified, its distance to the shore was measured, and the vegetation at the point nearest to each of these focal birds was scored subjectively between 1 and 3 (VI1 = no vegetation, open landscape; VI2 = partly vegetated; VI3 = fully vegetated; see Fig. 1). Finally, the number of individuals in each of these sub-sections was noted, converted to density and entered into the database.

The (fixed) effects of flock size (the natural logarithm transformed number of flamingos, ln(N)) and the categorical variable Vegetation Index (VI) on the distance of the focal bird to shore was tested with a generalised linear mixed model, with flock identity (Flock ID) as a random effect, using the MIXED procedure and default options in SAS 9.4 (SAS Institute). As a *post hoc t*-test analysis revealed no significant difference in distance to shore between VI2 and VI3, these two vegetation categories were lumped together in a later version of the mixed model (summarised as no vegetation *versus* vegetation). Since the analysis demonstrated no explanatory power of ln(N) to the model, the final model then consisted of distance to shore as a function of VI consisting of two categories as the only fixed effect.

Results

Distance between individuals

For all flocks, the Ripley's K analysis showed that individuals were more dispersed than expected by chance at short distances, but clustered at greater distances. The point of crossover in this relationship was similar among all 15 flocks, at a mean of 0.70 m ± 0.06 (95% C.I.) identical to the mean inter-bird distances for all flocks (Fig. 5), suggesting a non-random pattern at very short inter-bird distances consistent with regular spacing within dense flocks.

Distance to shore in relation to predator threat

The mixed model Distance ~ Vegetation Index + ln(N) with Flock ID as a random factor showed a highly significant effect of

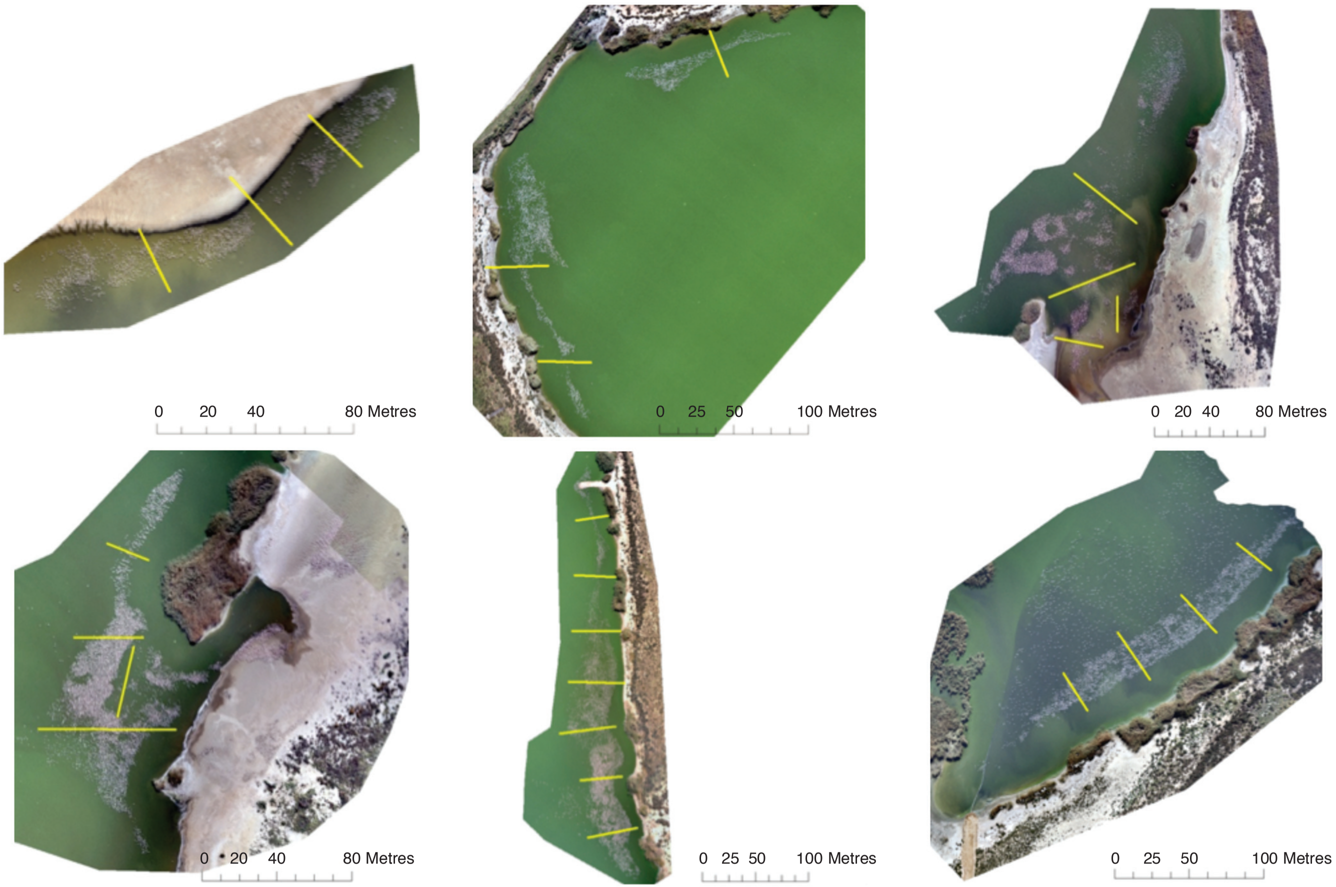

Figure 4. Illustrating the six other aerial images (in addition to Fig. 1) used during the study of Lesser Flamingos at Kamfers Dam in May 2006. Yellow lines indicate the divisions made within continuous groups of Lesser Flamingos to break flocks into smaller units for the analysis, as described in the text. Note that the pictures presented here are portrayed at different spatial scales, for clarity, as indicated on each image.

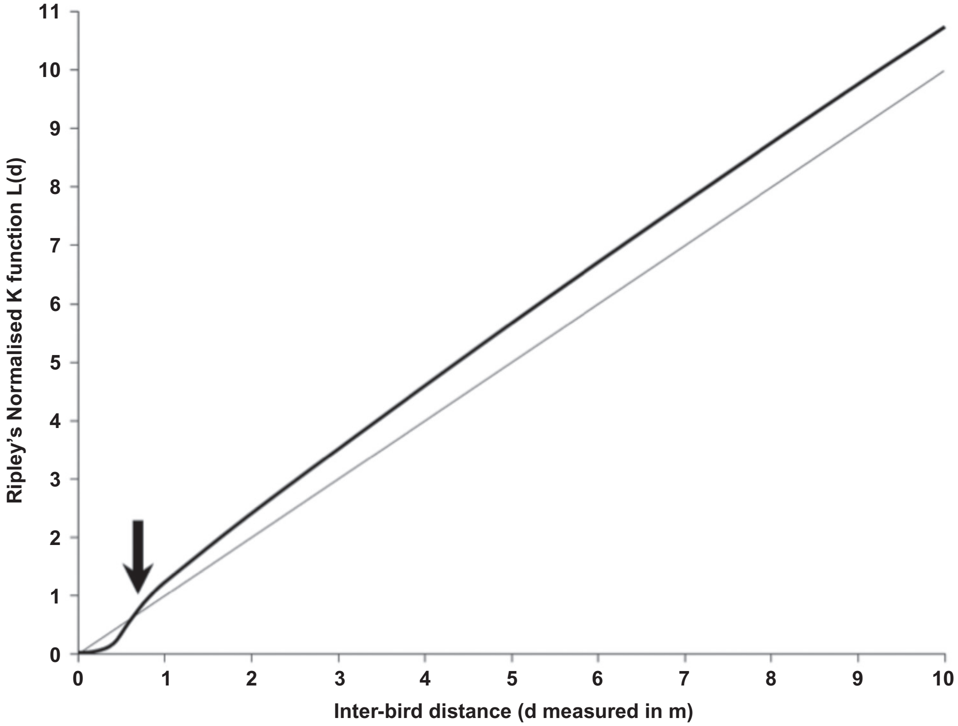

Figure 5. Example of output from Ripley's K analysis of inter-bird distances for one of the 15 analysed dense flocks of Lesser Flamingos generated from vertical imagery of Kamfers Dam in May 2006. The black line indicates the expected spatial distribution; the grey line shows the observed spatial distribution. Values below the expected imply dispersal; those above the line imply clustering amongst the objects. Note that the point of crossover approximates to the mean inter-bird distance in dense flocks (arrowed), implying regular arrangement at distances of < 0.7 m but clustering above that level.

vegetation index on flock distance from shore ($F_{2,21} = 18.28$, $P < 0.0001$; Fig. 6), with significant effects of flock as a random variable ($P = 0.025$), but no contribution from flock size ($F_{1,21} = 0.0$, $P = 0.97$, n.s.). The model predicted an estimated distance to shore of 4.1 m (95% C.I. = 1.3–6.9 m) for no vegetation, 10.0 m (95% C.I. = 7.3–12.7 m) for partially vegetated shorelines and 14.0 m (95% C.I. = 11.1–16.9 m) for shorelines with vegetation. *Post hoc* analyses demonstrated no significant difference between VI2 and VI3; hence the model could be reduced to a single fixed effect of the vegetation index, with two categories (*i.e.* vegetation/no vegetation). *Post hoc* *t*-tests showed the difference between these two estimates to be highly significant ($t_{23} = 5.94$, $P < 0.0001$).

Discussion

Distance between individuals

Lesser Flamingos that aggregated in the high-density stratum showed highly

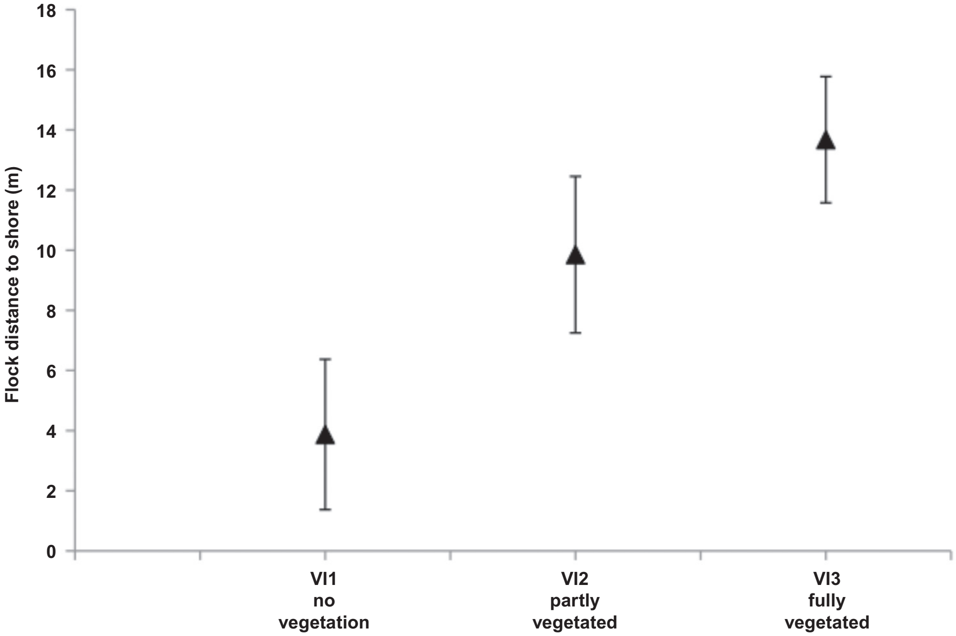

Figure 6. Mixed model estimates of mean flock distance to the shore (+ 95% C.I.s) in relation to shoreline vegetation type, from 40 dense flock sub-units of Lesser Flamingos at Kamfers Dam in May 2006.

distinctive spatial arrangements within these flocks. Individuals were more dispersed than expected (*i.e.* diverged from spatial randomness at a given distance) when the birds were within 0.70 m of each other in the images, but were slightly more clustered beyond this limit. One possible explanation for this geometry within the flocks is that individuals follow an ideal free distribution, which predicts that the flamingos would distribute themselves within the lake in such a way that each individual attains the same food intake rate (Sutherland 1983). Studies have shown that, in the short term, flamingo feeding activity in dense flocks can shift prey distribution but rarely causes local food depletion (Glassom & Branch 1997; Rodríguez-Pérez *et al.* 2007). The food supply at Kamfers Dam is considered to be super-abundant and mobile in the water column of the shallows (Anderson 2008), and as the flamingo flocks are highly mobile, this seems an unlikely explanation. What seems more likely is that this spacing arrangement is a manifestation of interference competition, where individuals maintain a certain distance between themselves and neighbours, so as to reduce lost feeding time in agonistic interactions; an extension of Conder's (1949) "personal space" concept. Inter-bird distance within flocks is maintained by movement towards another flock member resulting in that bird moving away (through avoidance or submission) without major loss of feeding time because of prolonged aggression. Although Yosef (1997) observed no aggression amongst feeding Greater Flamingos, his study flocks were more dispersed (with inter-bird distances of up to 30 m), than those considered here and American Flamingos *Phoenicopterus ruber* frequently resort to aggression in dense flocks (Bildstein *et al.* 1991; Schmitz & Baldassarre 1992b). It is not clear what causes the regularity of spacing observed here at Kamfers Dam, but it seems likely that this is the result of individuals attempting to maintain equal distances from each other to avoid loss of feeding time due to aggression, even if aggression may make some contribution to maintaining this spatial arrangement. Such spacing behaviour establishes a social limit on the maximum density of flamingos which can exploit a super-abundant prey source. Clearly, there remain major possibilities for studying the effects of food supply, food depletion and agonistic interactions on the spacing behaviour of Lesser Flamingos where they aggregate in such dense flocks.

Distance to shore

Flamingos using the artificial island on Kamfers Dam showed no avoidance of the shoreline, straddling the shallows, shoreline and land without pattern (Fig. 2). In contrast, all 15 flamingo flocks included in the analyses showed a consistent avoidance of the mainland shore around the entire lake (Fig. 4). Flamingo flocks kept a certain, and locally relatively constant, distance from the shore around the edge of the lake. Because the high-density stratum maintained constant high densities of flamingos along the edge closest to shore, we infer that the birds are showing strong avoidance of the shoreline. This is presumably as a "safety" measure, because of the threat from predation. This presumption was supported by the significantly greater distances observed from vegetated compared to the unvegetated open shorelines amongst the 40 flock sub-units. This supports our prediction that vegetated shorelines provide increased cover for predators, where detectability of their approach by the "many eyes" (Pulliam 1973) of flock members is likely to be much lower because of the impeded visibility compared to the shorelines devoid of cover. This contrasts strongly with other previous studies of bird species that use cover as refuge from predators, and which are reticent to forage in areas away from such cover due to the greater threat from predation, resulting in more time being invested in vigilance and less in feeding (Barnard 1980; Caraco *et al.* 1980; Diaz & Asensio 1991). In the case of the Kamfers Dam flamingos, the birds benefit from dense flocks providing "many eyes" and potentially predator dilution effects, enabling them to remain in food-rich, but exposed, patches away from risky environments through the distribution of flocks, albeit at loss to potential feeding habitat in those areas nearest the shore.

We would predict highest food concentrations in shallow waters because elevated water temperature, nutrients and wave action likely enhance photosynthesis and growth of the cyanobacteria, as well as the shallows offering optimal foraging depths for the birds. Bartholomew &

Pennycuick (1973) differentiated between high and low density foraging by flamingos in optimal and sub-optimal feeding habitats respectively. Mixed flocks of different flamingos in Argentina showed different depth preferences for different species, but none foraged in water deeper than 50 cm (Mascitti & Castañera 2006). It seems possible that deeper waters also likely formed the outermost limit on foraging by Lesser Flamingos at Kamfers Dam. Further studies of the relationship been water depth, food supply and the feeding distribution of Lesser Flamingos at the site are required to confirm these patterns.

There was no indication of an association between flock size and the distance to shore. This could be because, above a threshold size, flocking has a limited effect on the perceived risk of predation (either through detection or dilution) or because, in very dense aggregations, flamingos are simply unable to assess the size of their own flock. Alternatively, flocking in the Lesser Flamingo is more related to direct foraging benefits, than to an immediate reduction in predation risk. Nevertheless, Yosef (1997) found that smaller flocks of Greater Flamingos were more prone to re-locate *en masse* by flight than larger flocks in response to a given threat, confirming some threshold size for deriving a "safety in numbers" advantage.

We therefore conclude that Lesser Flamingos at Kamfers Dam probably aggregate due to the abundance of their food supply within the site (as found elsewhere), and cluster to densities up to a limit imposed by interference that regulates individual spacing within dense flocks. As internal flock densities are maintained to a sharp flock edge at a distance of between 4–14 m from the shore, assuming uniform food abundance, we conclude that the flamingos suffer effective habitat loss by almost never feeding within these distances of the mainland shoreline. We were able to show that this distance was positively related to the degree of vegetation cover along the section of shoreline, and therefore we suggest that this avoidance zone is caused by the perception of the degree of risk of predator approach (either terrestrial or aerial predators or both, which could potentially use such cover to conceal a predation attack). The conclusions from these analyses are limited by the lack of simultaneous assessment of the distribution and abundance of the food supply and their effects on the distribution and abundance of the birds in this study; such work is strongly recommended for future study. Given the relatively low cost of deployment of drone-mounted cameras, it is becoming easier to generate vertical imagery of flamingo flocks and to relate these to food density and water depth, in order to test more rigorously some of the hypotheses presented here.

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Photograph: Lesser Flamingos on the breeding island at Kamfers Dam, South Africa, by Mark D. Anderson.

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