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Structural organisation and dynamics in king penguin colonies

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Abstract

During breeding, king penguins do not build nests, however they show strong territorial behaviour and keep a pecking distance to neighbouring penguins. Penguin positions in breeding colonies are highly stable over weeks and appear regularly spaced, but thus far no quantitative analysis of the structural order inside a colony has been performed. In this study, we use the radial distribution function to analyse the spatial coordinates of penguin positions. Coordinates are obtained from aerial images of two colonies that were observed for several years. Our data demonstrate that the structural order in king penguin colonies resembles a 2D liquid of particles with a Lennard-Jones-type interaction potential. We verify this using a molecular dynamics simulation with thermally driven particles, whereby temperature corresponds to penguin movements, the energy well depth ϵ of the attractive potential corresponds to the strength of the colony-forming behaviour, and the repulsive zone corresponds to the pecking radius. We can recapitulate the liquid disorder of the colony, as measured by the radial distribution function, when the particles have a temperature of several $(1.4-10) \epsilon/k_B$ and a normally distributed repulsive radius. To account for the observation that penguin positions are stable over the entire breeding period, we hypothesize that the liquid disorder is quenched during the colony formation process. Quenching requires the temperature to fall considerably below $1 \epsilon/k_B$, which corresponds to a glass transition, or the repulsion radius to exceed the distance between neighbouring penguins, which corresponds to a jamming transition. Video recordings of a breeding colony together with simulations suggest that quenching is achieved by a behavioural motility arrest akin to a glass transition. We suggest that a liquid disordered colony structure provides an ideal compromise between high density and high flexibility to respond to external disturbances that require a repositioning of penguins.

Keywords: king penguin, molecular dynamics, 2D liquid, Lennard-Jones potential, radial distribution function, jamming, glass transition

 Supplementary material for this article is available [online](#)

(Some figures may appear in colour only in the online journal)

1. Introduction

Structural order is ubiquitous in animal colonies and has been described for example in flocks of starlings [1], schooling fish [4, 24], or groups of insects [2]. Structural order facilitates communication and navigation, protects against predators or helps to hunt prey.

While these are examples of a dynamic order, some groups of animals also display structural order in static constellations, for example burrows of prairie dogs [16], or colonies of fur seals [11]. Particularly interesting among animal colonies that display structural order are bird colonies during breeding, in particular king penguin colonies (*Aptenodytes patagonicus*). Breeding individuals conglomerate in dense colonies that can reach up to 500 000 breeding pairs [15]. Available aerial images of king penguin colonies suggest a seemingly ordered structure in the positions of individual animals, the existence of which has also been noted in the scientific literature, where breeding areas were described as ‘regularly spaced’ [7, 15]. However, a rigorous analysis of the structural order in a king penguin colony has thus far been lacking.

King and emperor penguins are the only penguin species that do not build nests [23]. Instead, the parents carry the egg on their feet. Unlike emperor penguins, king penguins are territorial [6, 17]. Once a pair has selected their breeding site, they defend a small territory of less than 1 m in radius with their beak and flippers against predators and other penguins [7], making it challenging for passing penguins to find a path through the colony with the fewest number of aggressive encounters [8]. Most intriguingly, despite the absence of nests, the positions of the individual breeding sites remain stationary within the colony, with an average displacement of only 1.3 ± 0.2 m during the entire incubation period of 2 months [17].

The aim of this study is to characterize and describe the structural order in a king penguin colony during the early stage of the breeding cycle, where most of the penguins are already incubating an egg. We record the spatial positions of several thousand individual animals and breeding pairs from aerial images and then analyse them with the radial distribution function, also known as the pair correlation function. We find that the colony structure resembles a fluid with short-range liquid order. Using a physical framework based on a Lennard-Jones-type energy landscape, we demonstrate that this liquid order arises from an interplay between repulsive and attractive interactions between neighbouring breeding penguins, whereby the territorial pecking radius leads to a repulsive potential, and space constraints and the need to protect against predators lead to an attractive potential that keeps the colony together [20]. Finally, we demonstrate that this liquid order is frozen in time by a glass transition that occurs during the breeding site selection process as new breeding pairs join the colony.

2. Material and methods

2.1. King penguin biology

Our study is based on aerial images taken during early December. During this month, adult penguins are found in

two different states of the breeding cycle. Penguins that succeeded in raising a chick in the previous year still feed their nearly grown-up chick and will not start to breed until January (late breeders). Penguins that failed to raise a chick in the previous year have already started breeding by December (early breeders). Some of them have established their breeding site and are incubating their egg, whereby the parents take turns. Other early breeders are not yet incubating but are looking for partners, are mating, or are establishing their territory. For this analysis, we select regions within the images that are free of chicks from the previous breeding cycle.

2.2. Images

We analyse a total of five high-resolution aerial images taken from a helicopter at an altitude of approximately 300 m above ground. All images were taken during the month of December of different years. Images #1–4 were taken from the Baie du Marin king penguin colony on Possession Island, Crozet Archipelago (S 46° 25.544', E 51° 51.673'). Image #5 was taken from the Ratmanoff bay colony, Kerguelen Archipelago (S 49° 14.154', E 70° 33.230'). Image #1 was taken on December 10th 2010 with a Nikon D300, showing 7073 adults and 539 chicks. Images #2 and #3 were taken on December 9th 2014 with a Canon EOS 50D, showing a total of 1560 adults and five chicks. Image #4 was taken on December 8th 2016 with a Canon EOS 7D Mark II, showing 4903 adults and 118 chicks. Image #5 was taken on December 15 2008 with a Nikon D300, showing 6501 adults and 104 chicks.

2.3. Video

We recorded a video (duration 1 h) of the penguin colony at Possession Island with a GoPro Hero2 camera placed at an elevated position of approximately 10 m overlooking the Baie du Marin valley. For the subsequent analysis of penguin positions using the software Clickpoints [13], videos are stabilized to correct for wind-induced drift using a template matching algorithm [3].

2.4. Data analysis

We analyse images of the central part of the colony where the topography is flat and therefore does not affect the spacing between penguins. Positions of the penguins are extracted from the images using a software tool (ClickPoints [13]), where we manually mark the pixel coordinates of the penguin feet. We distinguish between chicks (clearly recognizable by their brown colour) and adults. When two adults are closer than 0.45 m, they are classified as pairs, as discussed below. Correction for the camera perspective is performed by affine image transformation with a transformation matrix that we obtain from point correspondences of prominent landscape features (buildings, walls) seen in the Google Maps satellite images of the region [12].

Penguins are classified as neighbours using a Delaunay triangulation [9]. From this triangulation, we compute the Voronoi cell around each penguin, to visualize the region that

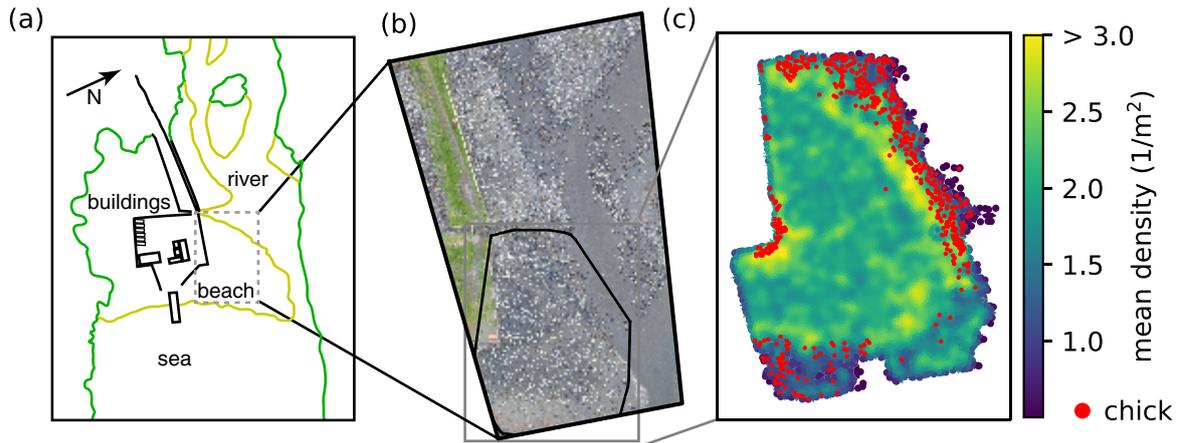


Figure 1. Organisation of the breeding colony. (a) Overview map of the Baie du Marin king penguin colony site. (b) Aerial image of the breeding site (December 10th, 2010). (c) Map of the local penguin density, smoothed with a Gaussian kernel (1 std = 1 m, chicks are included in the density calculation). Yellow colours represent higher densities, which are found at the border of the colony near the wall (left) and near the river (right). Red dots represent chicks. The density distribution for other colonies and years is shown in supplementary material B.

a penguin occupies. Penguins at the border of the image where not all neighbours are visible are excluded from the analysis to avoid bias.

2.5. Numerical modelling

Numerical ‘molecular dynamics’ simulations are carried out according to [22] on a system of $N = 100$ particles with number density ρ in a 2D box of length $L_x = L_y = \sqrt{N/\rho}$ with periodic boundary conditions. The particles representing either single penguins or the centre-of-mass of penguin pairs are initialized on a hexagonal grid with random velocities. Velocities are scaled so that the velocity of the centre of mass is 0, and the sum of their kinetic energies equals the thermal energy defined by the temperature T . The particle interactions are simulated with a Lennard-Jones potential:

$$U(r) = 4 \cdot \epsilon [(\sigma/r)^{12} - (\sigma/r)^6] \quad (1)$$

with energy well depth $\epsilon = 1$ and variable distance σ where the potential is zero. A constant value is added to $U(r)$ so that the potential vanishes at a cut-of distance $r_c = 5.0$ [21]. To account for different repulsion radii of the penguins, we choose a different σ_i for each penguin, drawn from a normal distribution around a mean σ with a standard deviation of $\Delta\sigma$. The dynamics of particle movements is simulated using a Leap-Frog integration. For the first 2000 time steps, velocities are rescaled every 10 time steps to keep the temperature constant until the system has reached a steady state. The next 6000 time steps are then used to average over the system’s properties: temperature, radial distribution function of particle distances, and pressure.

Simulations are carried out over a grid of different temperatures T , different values of σ , and different polydispersities $\Delta\sigma$. The grid point with the lowest squared error of the radial distribution function $g(r)$ is used as the best fit (for details on the evaluation of the radial distribution function, see

supplementary material A (stacks.iop.org/JPhysD/51/164004/mmedia)).

The interaction potential is characterized by a minimum energy ϵ of unity at a radial position $\sigma\sqrt[6]{2}$ that corresponds to the preferential distance (in units of m) between neighbouring particles. In the simulation, the density ρ of the particles is fixed by the average density of breeding penguins in a uniform region in the middle of the colony with no chicks ($\rho = 1.7$ animals m^{-2}).

The time in the simulations is given in units of $\sigma\sqrt{m/\epsilon}$. To calculate mean squared displacements (MSD) of particles over time, simulations were run for 600 000 time-steps with a dt of 0.001.

3. Results

3.1. Overall colony organisation

The Baie du Marin colony is situated in a valley with a seasonal river mouth and a small patch of beach. The beach provides space with varying degrees of suitability as a breeding ground for king penguins. Areas near the river have an increased risk of flooding, and areas near the valley sides have a rocky and uneven ground due to tussocks and cliffs, which may pose a problem for incubating birds (figure 1). Thus, breeding penguins are mostly found at the beach away from the river, whereas non-breeding penguins are ‘pushed away’ from the prime breeding area towards the river mouth (figure 1(b)). This is reflected by the distribution of penguin densities, with a lower density of approximately 1.5 animals m^{-2} at the sites where breeding penguins defend their territory, and a higher density of up to 3 animals m^{-2} in areas where non-breeding penguins gather (figure 1(c)). For the same reason, chicks from the previous breeding season can only be found near the border regions that are less suitable for breeding (figure 1(c)).

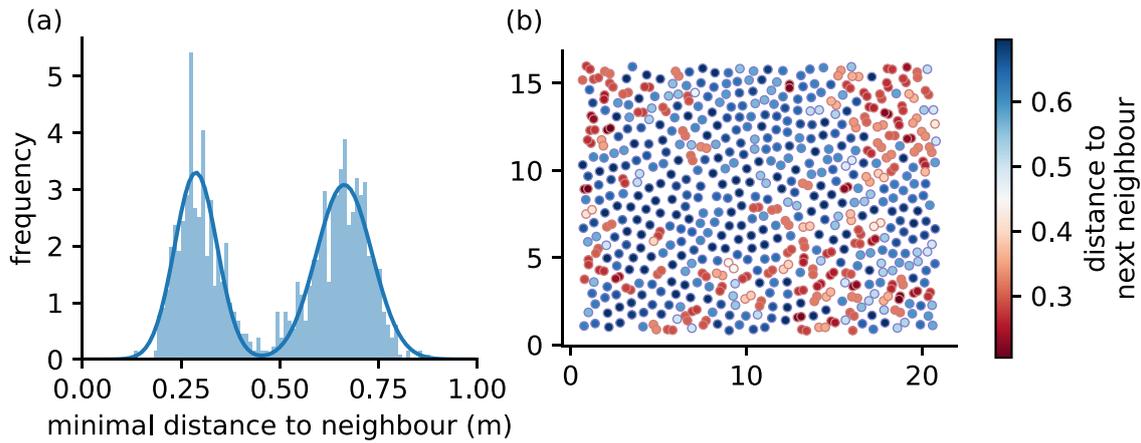


Figure 2. Separation of solitary penguins and couples. (a) Histogram of the minimal distance of each penguin to its neighbours (data are taken from the two images from 2014, Baie du Marin, as shown in figure 4(a)). The histogram separates in two Gaussian-like distributions centred at 0.29 m and 0.67 m. (b) Colony structure with penguins denoted by circles. The distance of each penguin to its closest neighbour is colour-coded.

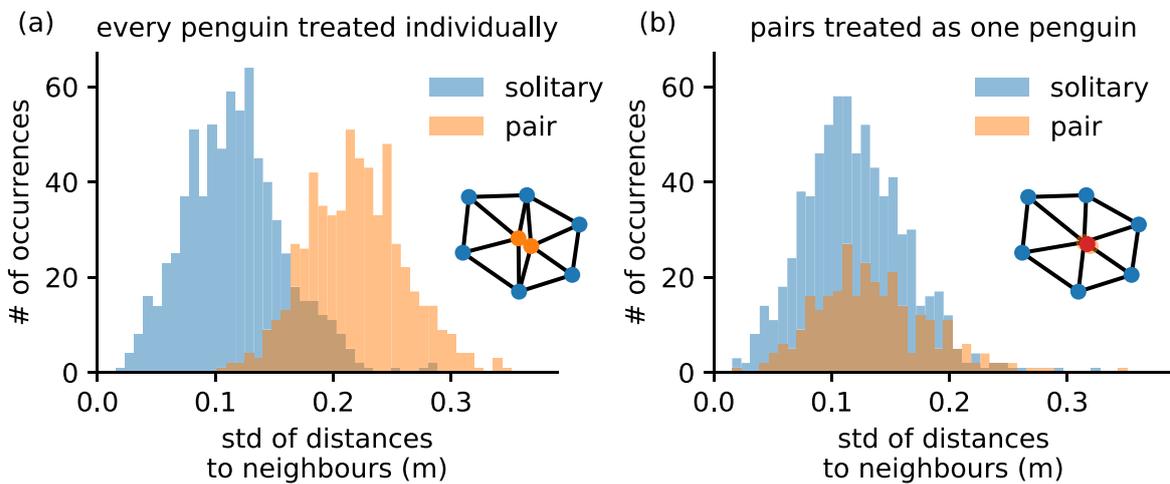


Figure 3. Distance distribution between neighbouring penguins. (a) Distance distribution of solitary penguins (blue) and penguins belonging to a pair (orange) to their immediate neighbours (data from 541 penguins). Penguins belonging to a pair show a higher standard deviation and thus disorder. (b) If the positions of penguins belonging to a pair are averaged (centre-of-mass), the disorder vanishes, and both solitary penguins and pairs show the same order.

3.2. Solitary penguins and couples in the colony

We find that the distance of each penguin to its closest neighbour shows a distinct, non-overlapping bimodal distribution (figure 2(a)), corresponding to penguins standing alone (‘solitary’) and two penguins standing close to each other (‘pair’). As the distribution of minimal neighbour distance d (figure 2(a)) has a clear minimum at 0.45 m, we can reliably classify penguins as solitary penguins when $d > 0.45$ m, and as pair when $d < 0.45$ m. Penguin pairs have an average separation of 0.29 m compared to a nearest neighbour separation of 0.67 m between solitary penguins. A spatial map of minimal distances confirms that the bimodal distribution arises from a separation in solitary penguins and pairs, and not from dense clusters of more than two penguins (figure 2(b)).

It has been previously established [23] and confirmed by on-land observation during the study period that solitary penguins are breeders, currently incubating an egg, where the

partner is not present in the colony and is probably foraging or resting outside of the colony core, while penguin pairs are breeding partners that interact for various reasons including mating or interactions associated with the egg exchange.

Distances between solitary penguins to their immediate neighbours have a standard deviation of 11 cm, or 17% (blue histogram in figure 3(a)). Distances between either penguin from a pair to its immediate neighbours (that includes their surrounding solitary penguins as well as their partner) have a much higher standard deviation of 22 cm. This is expected because the partner penguin is by definition much closer than the surrounding solitary penguins (orange curve in figure 3(a)). However, when we compute the centre position of a pair and then treat each pair as one penguin, these differences vanish, and both distributions of standard deviations collapse (figure 3(b)). This finding suggests that penguin pairs do not alter the regular structure of the colony and do not introduce additional

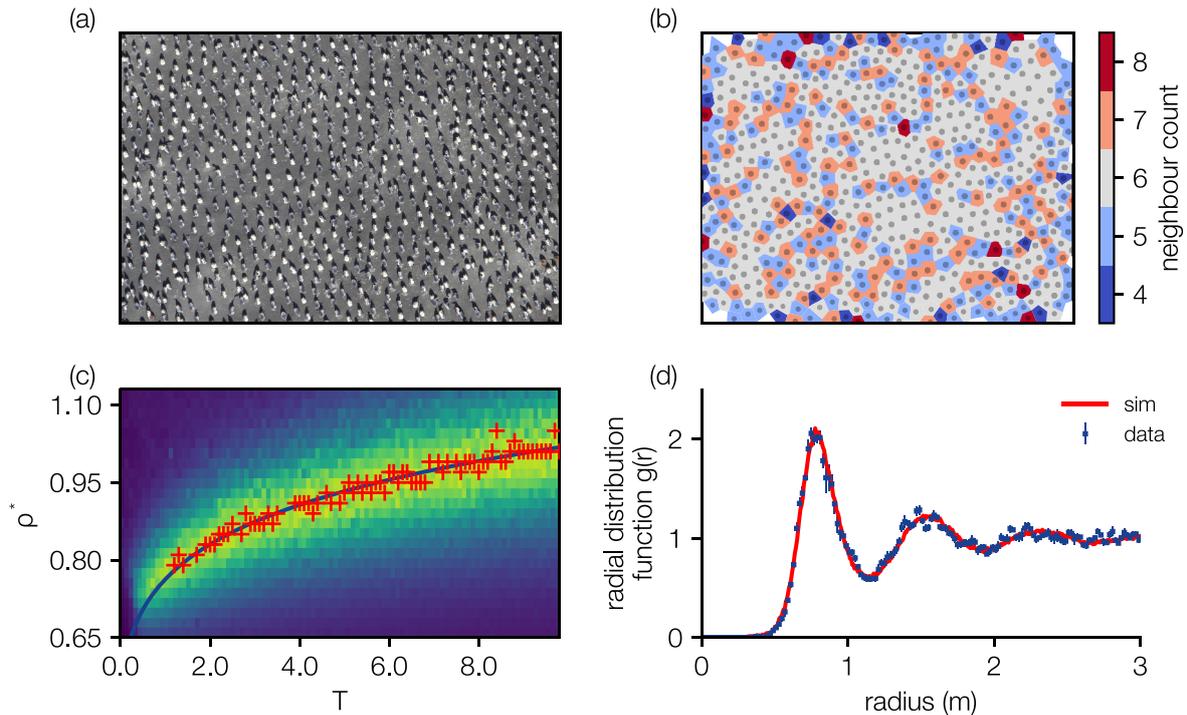


Figure 4. Colony structure. (a) Aerial image of the breeding colony (December 9th 2014). (b) Number of neighbours (colour coded Voronoi region) of each penguin (black dot). Most penguins have six neighbours. Five and seven neighbours occur predominantly in alternating bands. (c) Quality of fit for different combinations of T and ρ^* . Colours correspond to the squared error of the fit (blue: poor fit, yellow: good fit). Best fit combinations (red crosses) from independent simulation runs form a power-law relationship according to $\rho^* = 0.75 \cdot T^{0.13}$. For a visualisation of the system state in the fitted parameter range, see supplementary material H. (d) Mean penguin density around every penguin (radial distribution function, blue circles). The density shows a short-ranged periodic structure. Simulation of a Lennard-Jones fluid (red line) reproduces the data.

disorder. We obtain similar results over different years and for different colonies (see supplementary material C). For all subsequent structural analyses, the centre-of-mass of the two penguin positions forming a pair are computed and used instead of the position of each of the two penguins.

The spatial distribution of solitary penguins and pairs (figure 2(b)) suggests that penguin pairs tend to cluster. To quantify this, we compute for each penguin position (for pairs, the centre position is used) the fraction of neighbours that are pairs. If pairs are distributed randomly throughout the colony, the fraction of pair neighbours should on average be the same for solitary penguins and pairs. However, we find that 45% of the neighbours around a pair are other pairs, whereas only 16% of the neighbours around a solitary penguin are pairs, demonstrating that pairs in a penguin colony tend to cluster.

4. Colony structure

The position of penguins in the breeding areas appears approximately hexagonally ordered (figure 4(a)). We quantify the neighbourhood relationship between penguins using a Delaunay triangulation, which identifies the direct neighbours of each penguin. We find that about 53.0% of the penguins have six neighbours, 42.7% have five or seven neighbours, and 4.0% have four or eight neighbours (figure 4(c), histogram in supplementary material D). Penguins with six neighbours are found in small clusters that are separated by chains

of penguins with alternating five and seven neighbours. Such a neighbourhood arrangement is typical for a liquid [10]. The number of neighbours correlates weakly with the distance to the nearest neighbour, both for solitary penguins and for pairs (supplementary material D).

To quantify the order within the colony, we compute the radial distribution function [19], which is a measure of the density of penguins found within a circular shell around each single penguin of a given radius (figure 4(b)). The density is zero up to a radius of 55 cm, which confirms the impression from the aerial images that every penguin is surrounded by an empty region. The density reaches a peak at a radius of 0.73 m, which corresponds to the mean distance between two neighbouring penguins. At a radius of 1.2 m, the density reaches a local minimum. A second but smaller maximum is seen at 1.5 m, and a second faint minimum at 1.9 m, beyond which no further periodic density fluctuations are detectable. This result indicates that the ordered structure within a king penguin colony is of short range. Such short range order is typical for liquid systems. Similar radial distribution functions that closely follow liquid order can be seen for different years (2008, 2010, 2016) and across different colonies (Baie du Marin and Ratmanoff, supplementary material E).

To test the degree to which a penguin colony resembles a liquid system, we perform a molecular dynamics simulation of a 2D particle system with Lennard-Jones interactions [22] (figure 4(b)). The particles have an attractive potential ϵ that

corresponds to the strength of the colony-forming behaviour, and a repulsion radius σ that scales with the pecking radius of the penguins. Since we do not know ϵ and σ for king penguins, and since we assume an individually variable pecking radius, we perform the molecular dynamics simulation with three normalized parameters: a temperature in units of ϵ/k_B that corresponds to the kinetic energy of penguin movements, a relative density of penguins ρ^* in units of $\rho\sigma^2$ whereby the true density ρ is extracted from aerial images, and a standard deviation of the repulsive zone $\Delta\sigma/\sigma$ that corresponds to the inter-individual pecking radius variability.

We find that the radial density fluctuations in the penguin colony closely follow the predictions for a Lennard-Jones liquid with a $\Delta\sigma/\sigma$ between 20% to 30%, a temperature larger than $1.4 \epsilon/k_B$ and a relative density ρ^* above 0.8. Interestingly, combinations of temperature and relative density that best fit the measured data follow the empirical relationship $\rho^* = 0.75 \cdot T^{0.13}$ (figure 4(c)). This means that the system can dynamically sustain its liquid (dis)order over a large range of temperatures and relative densities. At the lower end of the spectrum (moderate temperatures T of order 1), the penguin colony resembles a typical liquid with a relative density of around 0.8 [21]. At the higher end of the spectrum (T above 4.43), the penguins exceed a relative density of $\rho^* = 0.916$ that corresponds to the maximally achievable relative density of incompressible 2D spheres (see supplementary material F), implying that penguins stand on average closer to each other than their preferred distance.

5. Colony dynamics

Since the penguins' positions in a breeding colony are stationary, the liquid disorder must have been kinetically arrested by a phase transition. Given the wide spectrum of possible temperatures and densities that can account for the observed colony disorder, two distinct scenarios are possible: if the colony is in a state of high temperature and high density, kinetic arrest can be achieved by lowering the temperature while maintaining a high density. This corresponds to a glass transition. If the colony is in a state of moderate temperature and density, kinetic arrest can be achieved by increasing the relative density while maintaining a moderate temperature. This corresponds to a jamming transition. Considering that breeding penguins move little and defend their breeding site fiercely, mixed strategies with a combined decrease in temperature and increase in density are also conceivable.

To gain better insight into the mechanism that leads to kinetic arrest in a breeding penguin colony, we performed simulations of particle trajectories for different temperatures and relative densities, and compared the results with the mean squared displacements (MSD) of penguins measured from video recordings. For all parameter combinations of temperature and relative density that are consistent with liquid disorder (see figure 4), the simulated MSDs show a ballistic regime (slope = 2) at small times ($\Delta t < 10^{-2}$) (see figure 5) that change into a diffusive random walk (slope = 1) for larger time lags. When the temperature is decreased

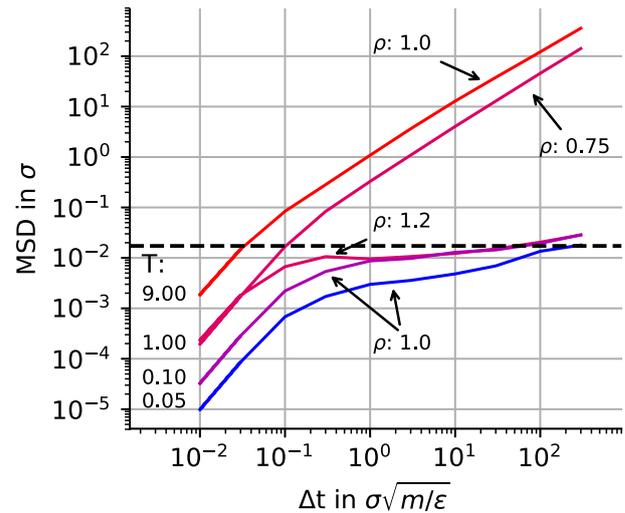


Figure 5. Simulated mean squared displacement (MSD) of particles for different temperatures (9–0.05 ϵ/k_B) and different relative densities ($\rho^* = 0.75, 1.0, 1.2$). The MSD starts with a ballistic regime (slope 2) for $\Delta t < 10^{-2}$ that changes at larger Δt to a diffusive regime (slope 1) or a plateau (slope 0), depending on temperature and relative density. For comparison, the upper limit of the plateau MSD in breeding penguins as measured from video recordings is indicated by the dotted line.

(corresponding to a glass transition), or when the density is increased (corresponding to a jamming transition), the particles are caged by neighbouring particles and the MSD reaches a plateau (slope = 0) at larger time lags. The plateau value of the MSD decreases with temperature, and this allows us to roughly estimate the corresponding temperature of breeding penguins by measuring their MSD over time from video recordings (supplementary material F). We find that penguins move by less than 9 cm over a time course of 10^2 s, corresponding to an apparent temperature around or below $1 \epsilon/k_B$, which is consistent with a glass transition. A low apparent temperature together with a density below a jamming transition is also in agreement with video recordings where breeding penguins appear immobile over extended time periods. This immobility is also seen for penguins at the colony edge that are free to move to less dense locations, as well as for penguins that are disturbed by an elephant seal (supplementary video 1).

6. Discussion

In this study, we analyse aerial images of two breeding king penguin colonies. We find that solitary penguins and pairs maintain a liquid-type order with a loosely hexagonal structure, where most penguins are surrounded by six other individuals. Penguin pairs occupy the same area as solitary penguins. Moreover, penguin pairs are not randomly distributed across the colony but are spatially clustered.

The core of the colony is more homogeneous and less dense than the border, where non-breeding adults are crowded and mixed with chicks from the previous breeding cycle.

This pattern is consistently observed over multiple years (2008, 2010, 2014, 2016) and at both locations (Crozet and Kerguelen). Therefore, all structural analyses presented in this study are performed only on the core regions of the colony.

Our analysis is based on the x - y coordinates of several thousand breeding penguins. To quantify the structural order of the colony core, we follow the strategy outlined in [5, 14, 26] and compute the radial distribution function of inter-penguin distances, which is a robust and easily interpretable measure of local structural order.

Strikingly, we find that the radial distribution function for king penguins shows clear peaks, in contrast to previous attempts to uncover structural order in rockhopper penguin colonies [14] and starling flocks [5] where no such peaks are visible. The radial distribution function of king penguins, however, shows only two clearly discernible local maxima and minima, which closely resembles the short-range order found in a 2D liquid system such as a Lennard-Jones fluid.

A Lennard-Jones fluid is characterized by two free parameters, the temperature of the system and the particle interaction radius. To extract these two parameters for a king penguin colony, we perform a molecular dynamics simulation of particles with a Lennard-Jones interaction potential. Note that the number density is not a free parameter in our simulation but is given by the observed penguin density. We then fit the radial distribution function of the simulated particle positions to the penguin data by varying the temperature, and the mean and standard deviation of the particle interaction radius.

From our simulations, we find two striking and unexpected features. First, the relative standard deviation of the particle interaction radius of around 25% is considerably larger than the relative standard deviation of the inter-individual body size of the penguins, which is estimated to be less than 5% [23]. Hence, the particle interaction radius cannot solely be determined by the anatomical pecking radius of the penguins but must also be modulated by individual preferences. Second, the same liquid disorder that we find in a penguin colony can be achieved in the simulations using a large range of temperatures and relative densities, as long as the temperature is above $1.4 \epsilon/k_B$ and the relative density follows an empirical power-law relationship of the form $\rho^* = 0.75 \cdot T^{0.13}$. Given that the penguin positions in a breeding colony are not dynamic but highly static and stable within ± 1.3 m over time scales of weeks to months [17], our findings of a large range of possible temperatures and relative densities suggest that the liquid disorder in a breeding king penguin colony can be quenched by multiple ecologically plausible strategies, namely by decreasing the temperature (positional movements) below a glass transition temperature [25], by increasing the repulsion (pecking) radius and hence the relative density beyond a jamming transition [18], or by a combination of both. A comparison of mean squared displacements from molecular dynamics simulations with measured penguin trajectories from video recordings suggest that penguins are kinetically arrested by a glass transition. Indeed, breeding penguins appear rooted to their chosen breeding spot and do not move even in the event of substantial external disturbances e.g. by elephant seals (supplementary video 1). This is also the reason why such disturbances

remain localized and do not propagate beyond a distance of one pecking radius.

This physical picture suggests the following scenario of how a breeding colony forms: first, the most favourable sites are occupied by early breeders. As more penguins join this seed of early breeders, the colony becomes denser and grows while non-breeders are pushed to the periphery. This colony growth can be pictured by a cooling of ‘gaseous’ free-moving penguins with an initially high thermal energy. Upon joining the breeding colony, the penguins establish and defend their breeding spot, which corresponds to lowering their thermal energy and increasing their relative density. The low equivalent thermal energy together with a repulsive zone quenches the system and prevents its annealing to a crystalline lattice with long-range order. Such a sequential growth of the breeding colony with layers of penguins that are in similar stages of the breeding cycle is also consistent with our observation that penguin pairs are locally clustered.

A liquid state of the colony can be seen as a compromise between density and flexibility. A gas-like state would offer a high degree of flexibility, meaning that penguins could walk freely through the colony because the density is low, but at the same time this requires considerably more breeding space for the colony. By contrast, a solid state would allow for only a marginal gain in density compared to a liquid state while making it virtually impossible to mend vacancies and local disturbances. Our data confirm that a liquid-like colony structure provides sufficient flexibility to adapt to internal and external changes. For example, a pair losing or abandoning their egg leaves a vacancy that is quickly filled, presumably by penguins that had occupied a less preferred breeding spot. This is possible since king penguins carry their eggs on their feet and do not build nests. The observation that nest-building rockhopper (*Eudyptes chrysocome*) breeding colonies show a nearly featureless radial distribution function akin to gas like order [14] may thus be attributable to their inability to repair vacancies.

Our findings of liquid disorder and glassy dynamics can also be recapitulated with Lennard-Jones particles with a repulsive potential in the absence of any attraction. However, without an attractive potential, penguins would randomly choose a breeding spot arbitrarily far from other breeding pairs. While the terrain dictates a natural boundary that encloses the colony, field observations demonstrate that the terrain is not randomly filled at the beginning of the breeding season but that breeding pairs tend to cluster even while large parts of the suitable breeding space is void of breeders. Moreover, we see dense clustering also in the Ratmanoff colony where only the beach serves as a boundary. Therefore, we include an attractive potential in our simulations to account for clustering in the absence of rigid boundaries.

In summary, we report unexpected analogies between the collective behaviour in a breeding king penguin colony and a simple physical system of thermally driven particles with Lennard-Jones interactions. While we do not expect that a Lennard-Jones interaction potential describes the ‘true’ force-distance relationship between neighbouring breeding penguins, the generic picture of repulsive, thermally driven

particles that undergo a glass transition recapitulates both the structure and dynamics of a breeding colony.

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