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Evidence of intra-specific competition for food in a pelagic seabird

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The factors affecting the population dynamics of seabirds have long intrigued biologists^{1–5}. Current data suggest that density-dependent depletion of prey during the breeding season may regulate population size^{6–9}. However, much of the evidence for this has been circumstantial, and the underlying mechanisms are unclear^{5,10}. Here, we show that the per capita population growth rates of northern gannet *Morus bassanus* at colonies in Britain and Ireland have declined with increasing population size. Furthermore, direct observations reveal that the mean foraging trip duration of breeding gannets is positively correlated with colony size, both among colonies of different sizes in the same year, and within colonies as they change in size. To understand this phenomenon, we have developed a model which demonstrates that disturbance of fish alone can readily generate conditions under which gannets at larger colonies have to travel further to obtain food.

Some researchers have proposed that density-independent factors may keep certain seabird populations below the levels at which density-dependent factors act^{5,11}, but others have argued that populations are likely to be regulated either through density-dependent breeding success^{1,6,9} or density-dependent mortality outside the breeding season². One mechanism that may generate density-dependent population growth was identified by Ashmole¹: adults foraging close to the breeding colony are likely to cause local prey depletion, so that birds from larger colonies will have to travel further to find food for their chicks than birds from smaller colonies. In support, consistent negative correlations between colony size and numbers at neighbouring colonies have been found⁶, indicating that even seabirds foraging in areas with high marine productivity may compete for resources. However, the causes of this higher-order relationship are unclear. For instance, some authors have questioned whether seabirds could take sufficient fish to cause significant depletion¹², while others have suggested that negative correlations of this nature can at least in part be explained by a tendency of large islands to be far apart¹³.

To evaluate the validity of Ashmole's population regulation hypothesis it is essential to first establish whether seabird populations actually exhibit density-dependent growth. Although smaller black-legged kittiwake *Rissa tridactyla* colonies tend to grow proportionately faster than larger ones¹⁴, the evidence for density-dependent growth in seabird species is extremely limited. The northern gannet *M. bassanus* is a good model species both to test for density-dependent growth, and to evaluate the validity of Ashmole's specific mechanism for several reasons. First, many colonies in Britain and Ireland have been expanding in size over the past century (in part owing to a reduction of persecution¹⁵, but perhaps also owing to increased food availability¹⁶), thereby providing an ideal opportunity to test whether per capita population changes are indeed density-dependent. Second, satellite tracking of breeding birds has shown that foraging range is very closely correlated with trip duration in this species, so that the distances travelled by adults can be accurately estimated from observed trip durations^{17,18}. Finally, the gannet feeds mainly on pelagic shoaling fish^{17,19} by plunge diving for prey^{19,20}, and currently occurs in

colonies which range in size from hundreds to tens of thousands²¹, providing the opportunity to investigate directly the effects of colony size on trip duration, and hence foraging range.

To test for density-dependent population growth, historical data on the estimated population sizes of gannets at 17 of the 18 British and Irish colonies were collated (see Methods). Time series analysis²² of the longest unbroken series of yearly censuses at seven different gannetries (see Methods) identified significant density-dependent population growth at three of these colonies (Fig. 1; Bempton $b = 0.9203$, $n = 16$, $P < 0.05$; Fair Isle $b = 0.8365$, $n = 25$, $P < 0.02$; Troup Head $b = 0.7708$, $n = 11$, $P < 0.005$). More gannet colonies were censused in Britain and Ireland in 1984/85 and 1994/95 than over any other period, so we have also estimated the per capita growth rates of gannet colonies over this decade. This between-colony comparison once again showed that the per capita growth rates of colonies declined significantly with colony size (Fig. 2, $r = -0.853$, degrees of freedom, d.f. = 13, $P < 0.001$). These findings are consistent with previous observations by Nelson¹⁹, a preliminary analysis of Scottish colonies²¹ and an earlier analysis of the growth of 34 gannet colonies (R. Moss, S.W. & M. P. Harris, unpublished work).

Crucially, a comparison of observations made of chick-rearing adults in the summer of 2000 at nine gannet colonies (see Methods) showed that there was a highly significant positive correlation between trip duration (hence foraging range) and square root colony size ($r = 0.898$, d.f. = 7, $P < 0.005$, Fig. 3), with trip duration increasing threefold between the smallest and largest

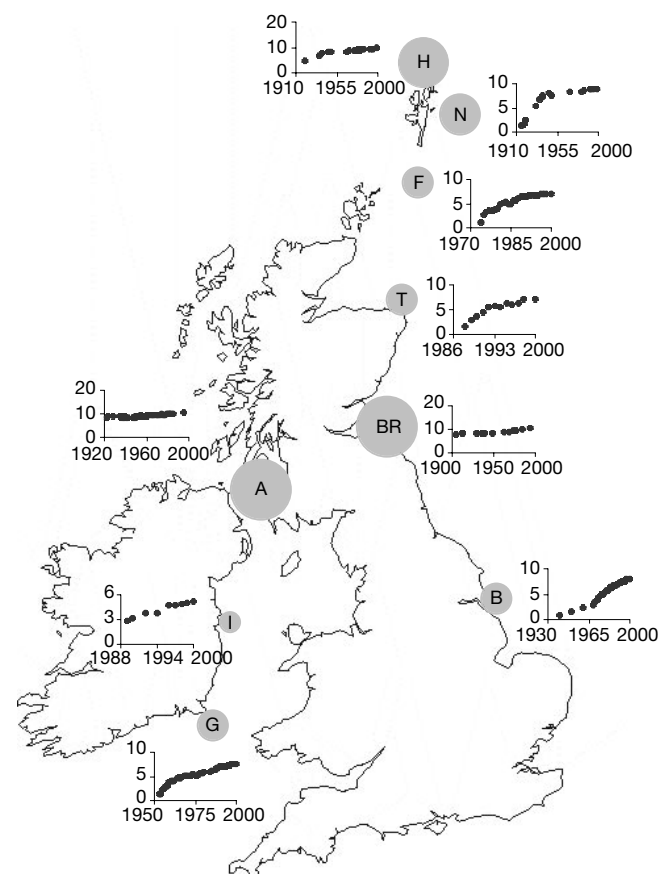


Figure 1 Location and size of gannet colonies. The current sizes, distribution and changes in gannet colony sizes over the past century at 9 of our 17 study colonies. (A, Ailsa Craig; BR, Bass Rock; B, Bempton; F, Fair Isle; G, Great Saltee; H, Hermaness; I, Ireland's Eye; N, Noss; T, Troup Head). Colony size was estimated as \log_e (apparently occupied sites). The area of the circle is proportional to current colony size (see Fig. 3 for actual values). Data on trip durations were collected at these 9 colonies.

population. Although pairs at the smaller colonies spent significantly more time together at the nest (square-root-transformed data $r = 0.725$, d.f. = 7, $P < 0.05$), the rate of provisioning of chicks by the parents still tended to decrease with increasing population size (square-root-transformed data $r = 0.662$, d.f. = 7, $P = 0.052$; log-transformed data $r = -0.671$, d.f. = 7, $P < 0.05$). Historical data on foraging trip duration at four of these colonies (Fig. 3) also fitted the same regression model extremely well (2000-only regression slope is 0.0492, standard error of the mean, s.e.m. 0.00907; pooled within colony regression slope for the four colonies is 0.0622, s.e.m. 0.0102, while a linear mixed model using combined data yielded a slope of 0.0548, s.e.m. 0.0128), indicating that the relationship within colonies between years is similar to our relationship between colonies within the same year. The generality of this relationship was further confirmed using data for St Kilda (the largest colony in the North Atlantic). In 1980, the colony held 40,000 apparently occupied sites and the average trip duration was around 21 hours (S.W., unpublished work). Finally, we note that of two pairs of colonies that were very similar in size (Great Saltee (G)

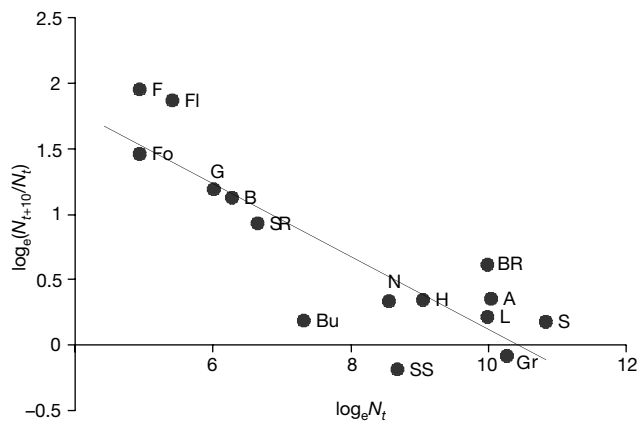


Figure 2 Density dependence in gannet colony growth. The relationship between $\log_e N_t$ (colony sizes in 1984/85) and $\log_e (N_{t+10}/N_t)$ (ratio of colony sizes in 1994/95 to 1984/85) is shown for 15 gannetries throughout the British Isles and Ireland. (Bu, Bull Rock; FI, Flannans; Fo, Foula; Gr, Grassholm; L, Little Skellig; S, St Kilda; SR, Scar Rocks; SS, Sule Stack; other colonies labelled as in Fig. 1.)

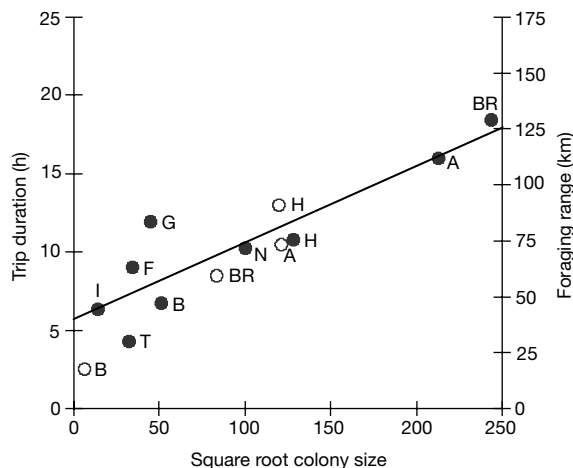


Figure 3 Gannets from larger colonies travel further to find food. The relationship between foraging trip duration and the square root of colony size for gannets is shown for the nine study colonies (labelled as in Fig. 1). Earlier data collected at four colonies (BR in 1966, B in 1972, A in 1975 and H in 1997) are represented by unfilled symbols. The line of best fit for 2000 data is shown.

and Bempton (B); Fair Isle (F) and Troup Head (T)) one was above the regression line of trip duration against colony size, and one was below it. The colonies that were above the regression line (G and F) are both approximately 50 km from other large colonies, while the colonies below the regression line (B and T) are both over 100 km away from other large colonies. This suggests that foraging birds from neighbouring colonies may to some extent compete for food.

To account for the relationship between trip duration and colony size, we have developed two complementary models in which shoals of pelagic fish show escape responses when they are attacked by diving gannets. If gannets are the primary source of disturbance and the escape response of fish involves some lateral movement, then shoals close to a colony will be attacked more frequently than those further away, and the overall tendency will be for fish shoals to diffuse outwards. Such movements readily generate a slowly growing ‘halo’¹, and we have found that under these conditions the mean foraging trip duration of gannets will increase with the square root of colony size. Yet some fish species may escape predation by swimming vertically downwards²³. Furthermore, factors such as currents or disturbance by other predatory species may effectively mix shoals to such an extent that halo patterns do not form clearly. In such cases, the geometry of central place foraging may explain our observations (Box 1). By integrating foraging rewards over a given flight path, it becomes clear that if gannets compete for available prey which is randomly distributed in discrete patches, then they should forage over approximately the same total area per bird to obtain the same amount of food, independent of colony size.

Box 1

Travel durations when central place foragers disturb prey

In this model, fish occur in discrete shoals of diameter s , which are randomly distributed with mean density d per unit distance. We assume that when shoals are disturbed by foraging gannets they become temporarily unavailable through some avoidance response (for example, sinking vertically and/or swimming away), but that they remain randomly distributed in space despite this disturbance. We consider a mainland colony of N pairs of gannets. Foraging gannets fly out to sea from the colony in straight lines with random directions, and each individual returns after they have gathered T units of fish biomass.

Let proportion p of the breeding adults leave the colony in search of food per unit time. Because gannets are in essence ‘central place’ foragers, the closer a shoal arises towards the colony the more birds are likely to encounter it. As a first approximation we have assumed that a mean proportion of $(s/\pi r)$ of gannets that leave the colony per unit time will encounter a shoal if it is at distance r from the colony (it is easy to show that the better approximation $2 \arctan(s/2r)/\pi$ yields very similar numerical results, but this function is less tractable analytically).

If g gannets encounter a given shoal (either simultaneously or in quick succession) per unit time, then let these individuals gain a mean reward of biomass $m(g)$. Here we have assumed that the immediately available prey are divided by the number of birds encountering the shoal, that is $m(g) = v/g$, where v is a constant. Nevertheless, functions with the highest foraging rewards per individual at non-zero gannet densities, such as $m(g) = 1/[g(w + c)]$, where w and c are constants, also generate similar conclusions so long as peak profitability arises for relatively few gannets. Under the above conditions, an individual gannet will gain net biomass B from continuing to forage for distance j where:

$$B = \int_{r=0}^{r=j} dv/(spN/\pi r) dr$$

If gannets cease foraging when $B = T$ then they should travel distance λ where

$$\lambda = \sqrt{(2spTN/dv\pi)}$$

such that the mean total travel distance (hence travel time) will be proportional to \sqrt{N} .

The area covered increases with the square of the mean foraging radius, which may explain why trip duration appears to be so closely correlated with the square root of colony size.

What are the implications of adults taking longer to find food at larger colonies? One possibility is that adults have to work harder at larger colonies and therefore experience higher mortality. Perhaps more importantly, if the average food load brought back to feed the young is constant among colonies, then chicks from larger colonies will receive less food per unit time than those at smaller colonies. Many seabird species exhibit reduced breeding success during years when food is scarce^{12,24}, but gannets rear only a single chick and our analysis of available data on gannet breeding success (see Methods) did not find a significant relationship between the mean number of chicks fledged per nest and mean colony size (Spearman $r = -0.086$, d.f. = 4, $P = 0.872$). Like gannets, Brunnich's guillemot *Uria lomvia* have a single egg clutch, and while fledging success similarly did not appear to change with colony size, this species had significantly lower fledging weights in larger colonies⁷. Finally, we note that there is evidence that gannets from large colonies recruit into smaller colonies¹⁹, so it is possible that the provisioning rates within colonies could play some role in influencing where birds choose to breed for the first time.

Although significant density-dependent changes in provisioning rates are likely to be demographically important, we do not know at this stage whether feeding rates have played a major role in influencing the population growth patterns that we have observed. Other density-dependent factors may also influence gannet dynamics, such as a gradual limitation of suitable breeding sites²⁵, or perimeter-restricted growth (R. Moss, S.W. & M. P. Harris, unpublished work), and it is possible that these factors interact to some extent. Density-independent factors (such as storm events) may also affect population size¹¹, but evidently these factors were not sufficient to obscure the underlying density-dependence in this case. Lower fish densities close to a breeding colony have already been observed for one species of seabird that forages inshore⁹ but it has long puzzled biologists how seabirds might show density-dependent competition for prey at sea when seabirds appear to contribute relatively little to total fish mortality²⁶. Here we have shown that density-dependent fish disturbance is sufficient to significantly reduce the mean profitability of fish shoals close to colonies, and thereby generate suitable conditions for intra-specific competition. Because such competition can arise without significant prey mortality, our findings may have important implications for the interactions of seabirds with commercial fisheries. □

Methods

Population censuses and detection of density dependence

The estimated population sizes of gannets at 17 colonies in Britain and Ireland (A, BR, B, Bu, F, FI, Fo, G, Gr, H, I, L, N, S, SR, SS and T; see Figs 1 and 2) were derived from published counts^{19,21,27–29} of apparently occupied sites and personal data. The minimum number of censuses per colony was ten, spanning a maximum period of 1902–2000. To test for density-dependent population growth within colonies, we used the distribution-free randomization test advocated in ref. 22, which involves calculating the slope b of $\log_e N_{t+1}$ versus $\log_e \log N_t$ (where N_t is population size at time t) and comparing this with gradients derived from 1,000 randomly permuted time series. As this method relies on unbroken series of censuses at fixed intervals, we were able to use this method for the yearly censuses taken at only seven colonies (A, 1947–1985; B, 1969–1984; F, 1974–1998; G, 1964–1980; H, 1974–1980; T, 1988–1998; SR, 1968–1976). To compare per capita population growth between colonies over the same period of time, we simply calculated the proportionate increase in gannet population size at 15 colonies between 1984/85–1994/95 (I and T were not considered as they were unoccupied in 1984/85).

Estimation of trip duration

Fieldwork took place during chick rearing (overall mean age of nestlings at each colony 7.4 weeks, range 5.0–9.9 weeks) at nine of the gannet colonies in Britain and Ireland (see Fig. 3). Nestlings were always attended by at least one parent. At each colony we observed approximately 20 breedings pairs with chicks (range 18–24) for a total time of 10–55 hours. By recording the arrival and departure times of adults at these nests we estimated the overall changeover rate of gannets per nest per day. The mean trip duration at each colony (hence time between feeds) was calculated by dividing the mean time available per

day for foraging (local daylight hours minus the mean time birds are together at the nest), by the estimated changeover rate. The historical data on trip durations in Fig. 3 were collated from personal (S.W.) and published data^{19,20}. All colonies were counted in 2000 with the exception of Bass Rock, Ailsa Craig, Hermaness and Noss which were last counted in 1994, 1995, 1999 and 1999 respectively. The population sizes of these colonies for 2000 were estimated using standard population growth trajectories²¹. Foraging range was related to trip duration by the following regression equations ($r^2 = 0.94$): $D = 7.05$ (s.e.m. ± 0.22) L , where D is the maximum distance (km) and L is the trip duration (h)^{17,18}.

Determination of breeding performance

Data on the breeding success of gannets at six separate colonies between 1986 and 1999 were obtained from a Joint Nature Conservation Committee (JNCC) published report³⁰.

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Calcitic microlenses as part of the photoreceptor system in brittlestars

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Photosensitivity in most echinoderms has been attributed to 'diffuse' dermal receptors^{1–3}. Here we report that certain single calcite crystals used by brittlestars for skeletal construction^{4,5} are also a component of specialized photosensory organs, conceivably with the function of a compound eye. The analysis of arm ossicles in *Ophiocoma*⁶ showed that in light-sensitive species, the periphery of the labyrinthine calcitic skeleton extends into a regular array of spherical microstructures that have a characteristic double-lens design. These structures are absent in light-indifferent species. Photolithographic experiments in which a photoresist film was illuminated through the lens array showed selective exposure of the photoresist under the lens centres. These results provide experimental evidence that the microlenses are optical elements that guide and focus the light inside the tissue. The estimated focal distance (4–7 μm below the lenses) coincides with the location of nerve bundles—the presumed primary photoreceptors. The lens array is designed to minimize spherical aberration and birefringence and to detect light from a particular direction. The optical performance is further optimized by phototropic chromatophores that regulate the dose of illumination reaching the receptors. These structures represent an example of a multi-functional biomaterial that fulfills both mechanical and optical functions.

Echinoderms in general, and especially the brittlestars (Ophiuroidea), exhibit a wide range of responses to light intensity, from a largely light-indifferent behaviour to pronounced colour change and rapid escape behaviour⁷. Figure 1 compares the appearance and the skeletal structure of two species of *Ophiocoma*, which represent the two extreme photosensitivity types. *Ophiocoma pumila* (Fig. 1a) shows no colour change and little reaction to illumination. *Ophiocoma wendtii* is a highly photosensitive species, and it changes colour markedly⁷, from homogeneous dark brown during the day (Fig. 1b, left) to banded grey and black at night (Fig. 1b, right). Another conspicuous behavioural response to light is negative phototaxis: *O. wendtii* is able to detect shadows and quickly escape from predators into dark crevices⁷, which they are able to identify from several centimetres away⁸. The latter reaction is particularly unexpected in these animals as the behaviour is usually associated with the presence of discrete photosensory organs. No specialized eyes have, however, been documented in brittlestars and their reactions to light have been linked to diffuse dermal receptors^{1–3}.

The sensitivity to light seems to correlate with the specialized skeletal structure of the dorsal arm plates (DAPs). These ossicles protect the upper part of each joint in brittlestar arms (Fig. 1c). Skeletal elements of echinoderms are each composed of a single crystal of oriented calcite shaped into a unique, three-dimensional mesh (stereom)^{4,5,9,10}. The diameter of the typical stereom in the DAPs of *Ophiocoma* is about 10–15 μm (Fig. 1d). In *O. wendtii* as well as in other photosensitive species⁶, the outer surface of the DAP stereom bears a characteristic array of enlarged spherical structures 40–50 μm in diameter (Fig. 1d, f). In cross-section they have a remarkably regular double-lens shape (Fig. 1g). The optical axis of the constituent calcite is oriented parallel to the lens axis and perpendicular to the plate surface⁹. The mean geometry of the lenses was inferred from the measurements of lens diameter (L) and thickness (t) in 20 random lenses sectioned through the centre (Fig. 1g):

$$t = 0.89L + 2.2 \quad (1)$$

with a correlation coefficient (r^2) of 0.91. Similar lenses were also

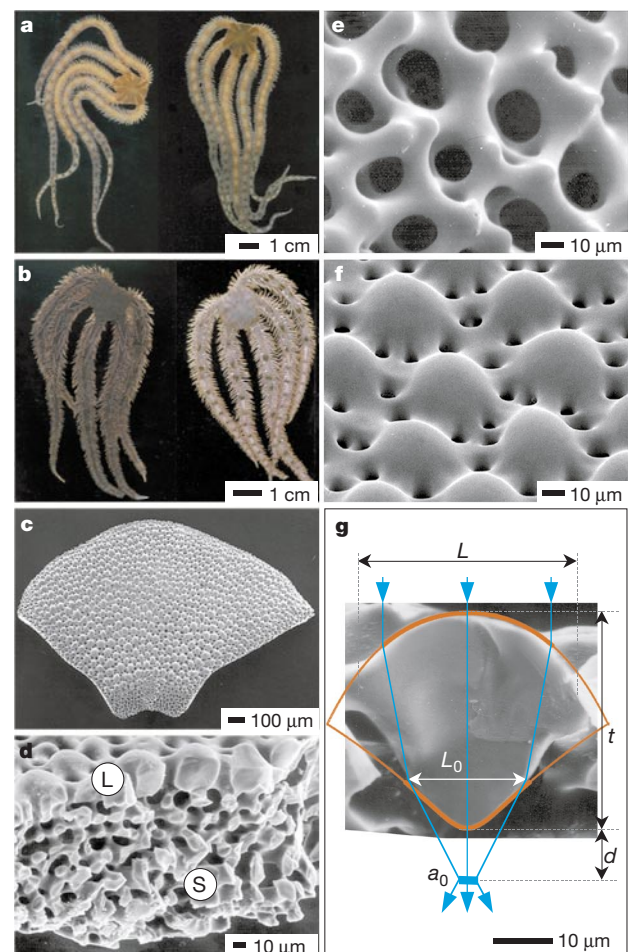


Figure 1 Appearance and skeletal structure of ophiocomid brittlestars. **a**, Light-indifferent species *Ophiocoma pumila* shows no colour change from day (left) to night (right). **b**, Light-sensitive species *O. wendtii* changes colour markedly from day (left) to night (right). **c**, Scanning electron micrograph (SEM) of a dorsal arm plate (DAP) of *O. wendtii* cleansed of organic tissue. **d**, SEM of the cross-section of a fractured DAP from *O. wendtii* showing the typical calcitic stereom (S) and the enlarged lens structures (L) that constitute the peripheral layer. **e**, SEM of the peripheral layer of a DAP of *O. pumila* showing that it lacks the enlarged lens structures. **f**, SEM of the peripheral layer of a DAP from *O. wendtii* showing the enlarged lens structures. **g**, High-magnification SEM of the cross-section of an individual lens in *O. wendtii*. Red lines represent the calculated profile of a lens compensated for spherical aberration. The operational part of the calcitic lens (L_0) closely matches the profile of the compensated lens (bold red lines). The light paths are shown in blue.