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"Ashmole's halo" is the term given to a zone of food depletion thought to surround the concentrations of predatory birds that exist in large seabird colonies. Philip Ashmole developed the hypothesis during studies of tropical terns. However, the idea has been widely applied outside the tropics, and most evidence for the hypothesis has been based on studies of high-latitude seabirds. We modelled some expectations for measurable variables, including foraging range, food availability and offspring development in relation to colony size for four seabird types (based on characteristics of the genera *Uria, Fratercula, Puffinus* and *Pterodroma*) and tested the model predictions against currently available data. We conclude that, although there is evidence for the existence of a zone of food depletion around seabird colonies, our model suggests that this zone is unlikely to be detectable for small colonies and especially for colonies of far-ranging species such as petrels and shearwaters. The hypothesis can be tested more effectively by measuring how food, feeding rates and feeding behaviour vary with distance from a colony than by comparing foraging at colonies of various sizes.

Key words: Seabirds, foraging range, food, energetics, central place foraging, *Uria, Fratercula, Puffinus, Pterodroma*

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 \mathbf{I}_{max} the British Ornithologist's Union sponsored and expedition sponsored and \mathbf{I}_{max} $\mathbf{v} \in \mathbb{R}^{2d}$ is the mid-Atlantic. One of the main objectives was to study the biology of the biology of the numerous seability the numerous seability \mathcal{A} especially the Sooty Tern *Sterna fuscata.* In the course of that

study, P_{max} as hole concentrations that large concentrations is that large concentrations in the idea that large concentrations is the idea that large concentrations is the idea that large concentrations is the idea of seability could depend on the food resources in the vicinity of the vicini breeding colonies. This zone of local food depletion has been termed "Ashmole's halo" (Birt *et al.* 1987). Ashmole further reasoned that the lowered food density would reduce the provisioning of nestlings and consequently lower reproductive output. He postulated that, as a colony expanded, it might reach a limit imposed by local resources and consequently that populations might ultimately be limited by

constraints on reproduction (Ashmole 1963, 1971). Ashmole's hypothesis differed from the ideas of his supervisor, David Lack, whose that seability that seability that seability that seability $\mathcal{L}_\mathbf{t}$ availability of food in winter (Lack 1966, 1968).

 A shmole was careful to restrict his hypothesis to the case of t "oceanic" (pelagic) species in the tropics. Because he found no evidence of population regulation regulation regulation \mathcal{P}_c by a lack of breeding sites, he argued that regulation by access to food was the most important factor. This regulatory effect was most likely to occur during breeding, because adherence to the breeding site restricted the foraging area and induced local competition for food supplies. Outside the breeding season, he reasoned that the birds could spread out to take advantage of the best feeding areas regardless of proximity to land and hence were less likely to be $\mathcal{L}(\mathcal{L})$ under competitive pressure. Specifically, he wrote: $\mathcal{L}(\mathcal{L})$

Competition for food around colonies will gradually become important as the population increases, so that the birds will find difficulty in raising young. Eventually the food shortage will become so acute that the production of young will decrease to the level [at which the population balances]. (Ashmole 1963)

Ashmole went on to point out that all the breeding biology traits that characterise pelagic seabirds (single-egg clutch, prolonged incubation and chick growth period, deferred maturity, $\frac{1}{2}$ be expected where intense competition for for for for for for for for for α breeding. Subsequently, Robert Ricklefs expressed the same idea, but in a more generalised form:

The direct relationship between fecundity and adult mortality [in birds] reflects primarily the density dependent feedback of adult survival on resources for reproduction. (Ricklefs 1977)

$T_{\rm eff}$ set of proposals about the regulation of set of set of set of seability $T_{\rm eff}$ populations has been termed "Ashmole's hypothesis," and has been very influential in seabird research. As summarised by Furness

 $\sqrt{\sqrt{1-\frac{1}{2}}\left(\frac{1}{2}\right)^2+\frac{1}{2}}$, Ashmole's hypothesis is that as $\sqrt{1-\frac{1}{2}}$ colony size (N) increases, foraging range (r) must increase through reduction in the availability of food close to the colony. At some point, the increased time spent in commuting to distant feeding

are as a few points for the extra feeding time caused for the extra feeding food availability $\mathcal{L}(\mathcal{L})$ close to the colony ("Ashmole's halo"), will be reflected in reduced

food delivery to the chicks. This condition will create selection for reduced brood size, slower growth rates and other energy-

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- conserving adaptations. Because the potential foraging area (A)
- increases as the square of foraging range ($\pi \bullet \gamma_A$
- flight speed and the energetic cost of transport. We also investigate \mathcal{L} the relationship between colony size and foraging distance. We investigate these questions for seability in four classes, $\mathbf{v} = \mathbf{v}$ all assumed to weigh one kilogram:
- • A "murre type" (e.g. *Uria* spp.), having an constant flapping flight and a nestling that requires continuous brooding by one or other parent, allowing only 12 μ for foraging by each parent; allowing by each parent; and these birds have a very high wing-loading (1.7–1.9 g/cm2 $\sum_{\mathbf{k}}^{\mathbf{k}}\mathcal{L}_{\mathbf{k}}$
- • A "puffin type" (e.g. *Fratercula* spp.), having an constant flapping flight and a nestling that is not brooded during the latter part of the nestling growth period, allowing both parents to
- for a grading 24 h/d; wing loading approximately 1.4 g/cm2imately μ • A "shearwater type" (e.g. *Puffinus* spp.), having a flight combining flat ping and gliding and a chick that is left unattended when \mathcal{L}_{max}
- large, allowing both parents to forage up to $\mathcal{L}_{\mathcal{A}}$ h/d; wing loading loading loading loading loading loading approximately 0.9 g/cm2
- • A "gadfly petrel type" (e.g. *Pterodroma* spp.) depending mainly on soaring flight and with both parents for $\mathcal{L}_\mathbf{z}$ wing-loading approximately $\mathbf{U} = \{ \mathbf{V}_i \}_{i=1}^n$
- Wing loading values were calculated from data in Tennekes (1996),
- corrected for all α as shown in Gaston (2004). To increase the Gaston (2004). To increase the corrected for all α comparability, we use \mathcal{U} and \mathcal{U} and \mathcal{U} are lating energy \mathcal{U}
- expenditure to body mass for different activities for adults, rather than published values for the energy expenditure of the selected genera. T able 1 shows values assigned for the four classes of seabird.
- We ignored the cost of thermoregulation. Young *Uria* are brooded continuously throughout growth at the colony (Gaston & Jones 1998)
- and both *Puffinus* and *Pterodroma,* whose chick is left alone during ی میں جین جین جین جین ریمیں جاتا ہے۔ جس راجیں جن ججین میں جام پر جاتی ہیں جین جین ہیں گیا گیا جاتا ہے اور اس ک **0**

 $\mathcal{F}_{\mathbf{S}}$ shows the relationships between the required feeding rates between the required feeding rates $\mathcal{F}_{\mathbf{S}}$ and foraging range for all four model species. These curves are truncated because, as the travel time approaches the travel time approaches the total time approaches the time available, feeding time becomes very short, and hence the required \mathcal{L}_max feeding rate begins to rise very steeply. We set the maximum foraging range at that distance at which the feeding rate is either 5 or 10 times the rate adjacent to the colony (D = 0 km as the "basal" **Colony size and foraging radius** \bar{I}

A strong contrast is evident between the auks and the petrels, with

maximum for the latter exceeding ranges for the latter exceeding that f former by approximately an order of magnitude. Like the puffin, those species do not need to brood their nestlings during the latter part of the growth period, freeing them for 24-hour foraging. They

also carry much larger loads, and concentrate the food transported transporte back to the nestling in the form of stomach oil, giving it a higher energy value. Consequently, a shearwater could travel up to $\mathcal{L}(\mathcal{A})$ is used source allowing a food source allowing a rate of \mathcal{A} for a source that would constrain murrer to a source that would constrain \mathcal{L} with $\frac{1}{2}$ kJ/h). This is the contract of the contract of

 $W_{\rm eff}$ seability seability of the maximum size of the chick varies and the chick varies are size of the chick varies as great deal between $\mathcal{L}_{\mathcal{A}}$ and between colonies (Gaston 1985). This is the colonies (Gaston 1985). This is variation has a large effect on the required data $\mathcal{E}(\mathcal{E})$ defines a large effect on the required data $\mathcal{E}(\mathcal{E})$ in turn affects the maximum foraging range. Fig. 4 is \mathcal{L}_1 in the maximum foraging range. Fig. 4 is \mathcal{L}_2 effect of varying the daily delivery. As the required daily delivery climbs, the maximum foraging range declines. For murres, the range of chick energy needs estimated for the typical range of chick

mass at departure suggests potential foraging ranges from 135 km $t_{\rm eff}$ km. The corresponding range for pure for pure for pure for pure for pure for p $\mathcal{F}_{\mathcal{F}}(F)$. Over the range from $\mathcal{F}_{\mathcal{F}}(F)$. Over the range from $\mathcal{F}_{\mathcal{F}}(F)$ energy needs, the relationship between energy needs and maximum foraging range is steeper for *Uria* than for *Fratercula,* so that a given change in feeding rate enables a greater change in foraging

range for the former, making flexibility in chick feeding rates a potentially more useful strategy for *Uria* than for *Fratercula.*

To model the relationship between colony size and foraging radius,

knowledge of how many parents could be sustained by the prey density around a colony is required. We previously calculated (see Figs. 2 and 3) the feeding rate gradient around a colony colona 0oraging $\mathcal{F}_{\mathcal{F}}$ and $\mathcal{F}_{\mathcal{F}}$ and foraging range is approximately logarithmic over the mid-range of observed colony size for both *Uria* and *Pterodroma* (Figs. 6 and 7). For *Uria,* maximum foraging range is estimated at 80 km for colonies of 10

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124 Gaston *et al*.: Ashmole's halo and population regulation in seabirds breeding \mathcal{P}_new is view. However, the Lack's view. However, the Lack's view. However, the Lack's view. outcome depended mainly on the difference between $\mathcal{O}_\mathbf{C}$ and resident terns (which constituted more than half the species considered). This comparison has not been pursued for other areas, something that might be very worthwhile.

 $\mathbb{E}_{\mathbf{X}}[\mathbf{C}]$ _{kk} =

Seabird life histories are characterised by low reproductive rates and high adult survival (Lack 1966, 1968). These attributes are characteristic of populations that are limited by resources, rather than by predations $\mathcal{L}_\mathcal{P}$ (MacArthur & Wilson 1967, Wooller *et al.* 1992). Nevertheless, many seabird populations are subject to periodic catastrophic mortality events, often associated with large-scale atmospheric or oceanic events (e.g. Ainley *et al.* 1988, Schreiber 2001). Also, year-to-year fluctuations in the availability of seability of seability of smaller prey (e.g. stocks of smaller prey (fishes) tend to be much greater than do changes in the populations of marine birds (Cairns 1992). The apparent contradiction between traits $\label{eq:2} \begin{array}{l} \mathbf{r} \\ \mathbf{r} \end{array}$ of prey fluctuations and catastrophic adult mortality on the other is one of $\mathcal{O}(n)$ that remains unresolved.

Lack (1966, 1966, 1968) considered that population regulation regulation regulation for \mathcal{L} seabirds probably occurred outside the breeding season. Studies \mathcal{S} the time seabirds seem to support se that view, because \mathbf{r} is seen seems to occur in winter to occur in winter \mathbf{r} (e.g. Meade 1974). However, those findings tell us nothing about \mathbb{R}^n how populations are regulated if the real constraints operate through reproduction or recruitment. Population models always indicate that adult survival is the most important demographic parameter \mathbf{r}_i in determining population trajectory. Again, that finding does not indicate that populations are controlled by controlled by controlled by changes in adults in adul survival—merely that population trajectories are strongly affected $\mathcal{L}_{\text{max}}(t) = \frac{1}{2\pi} \int_{0}^{\infty} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}} \int_{0}^{\infty} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}} \frac{1}{\sqrt{2\pi}}$ members of the colony with regard to feeding has been dependent of the colony $\mathcal{O}_\mathbf{C}$ the point that food is available for rearing only one offspring annually RAYNER, J.M.V. 1999. Estimating power curves of flying $\hat{i}_1 \cdot \cdot \cdot$ \cdot \cdot \cdot \cdot \cdot \cdot $I(.)$ 5. B_{1} .