ASHMOLE'S HALO AND POPULATION REGULATION IN SEABIRDS

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SUMMARY

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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*

INTRODUCTION

In 1961 the British Ornithologist's Union sponsored an expedition to Ascension Island in the mid-Atlantic. One of the main objectives was to study the biology of the numerous seabirds breeding there, especially the Sooty Tern *Sterna fuscata*. In the course of that study, Philip Ashmole conceived the idea that large concentrations of seabirds could deplete the food resources in the vicinity of their 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, who thought it likely that seabird populations were limited by the availability of food in winter (Lack 1966, 1968).

Ashmole was careful to restrict his hypothesis to the case of "oceanic" (pelagic) species in the tropics. Because he found no evidence of population regulation by either predators or diseases or 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 under competitive pressure. Specifically, he wrote:

> 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) might be expected where intense competition for food occurs during 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)

This complex set of proposals about the regulation of seabird populations has been termed "Ashmole's hypothesis," and has been very influential in seabird research. As summarised by Furness and Monaghan (1987; Fig. 1), Ashmole's hypothesis is that as 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 areas, or the extra feeding time caused by reduced food availability 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-

conserving adaptations. Because the potential foraging area (A) increases as the square of foraging range (A = π•r²), foraging range should be proportional to the square root of the population size.

In the first half of this paper, we explore some implications of Ashmole's hypothesis in a formal way by examining just how Ashmole's halo is created, and how foraging range and colony population size are related. In the second half of the paper, we review evidence from empirical studies that have a bearing on the hypothesis.

THE HYPOTHESIS

Models of Ashmole's halo

To clarify the logic underlying the interrelationships of the variables thought to combine in creating Ashmole's halo, we model an isolated seabird population breeding on an island surrounded by open ocean, each pair rearing a single nestling. Food is delivered to the nestling by both parents, working equally hard. We use a
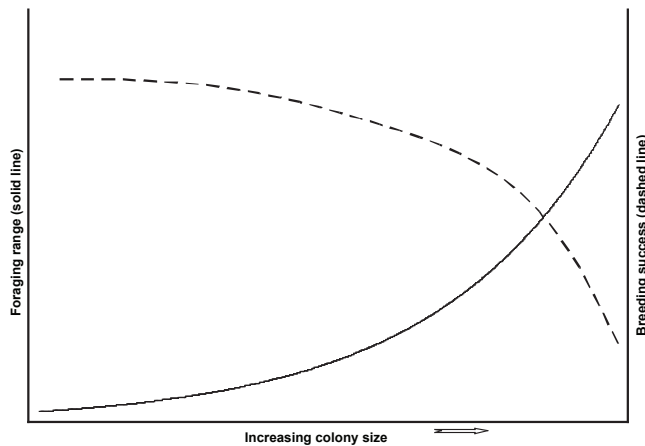
provisioning framework, which is based on central-place foraging models (see Ydenberg 2007).

The predictions are founded on two main assumptions: "energy balance" and "maximum delivery." The energy balance assumption is that each parent balances its energy budget over a foraging cycle (from colony departure to next colony departure). Therefore, it must, in addition to collecting prey for delivery to the nestling, spend time to capture and consume enough prey to power all of its own activities (Ydenberg 2007).

The maximum delivery assumption is that foraging decisions (e.g. where to capture prey, or the load size to deliver) are made to maximise the delivery rate of prey to the nestling, subject of course to constraints such as flight speed, the availability of prey, and metabolic rates. As a result of each parent seeking to do as well as possible, prey availability is reduced to the point that the attainable delivery rate from all potential foraging locations is equalised. The rationale is that if any location has a prey density such that the attainable delivery rate from that site is higher, foragers will concentrate there and reduce the prey density until the attainable delivery rate is equal to other places. It is clear that foraging locations far away from the colony must have higher prey density than those close to the colony; because of the greater transit time, more self-feeding is required to balance the energy budget of any forager that travels far, but less time is available to do so. Therefore the prey must be captured correspondingly more rapidly if the delivery rate is to be the same as that from locations closer to the colony. We consider that this effect underlies Ashmole's halo. Hamilton and Gilbert (1968) used a similar idea to explain the dispersion of starlings around a roost site, though they postulated that the return was equalised by varying the density of foragers rather than by the density of prey.

Here, we calculate the relative availability of prey at various distances from the colony that satisfies these assumptions and how that relationship is affected by species characteristics, such as the load-carrying capacity of the adults, the time required to brood the chick,

Fig. 1. Diagram of the Ashmole hypothesis: As a colony expands, depletion of local food supplies causes increased foraging range and reduced reproductive success. Adapted from Furness and Monaghan (1987).

TABLE 1
Model input variables for the four seabird types

Variable	Murre	Puffin	Shearwater	Gadfly petrel
From empirical observations				
Flight speed (m/s)	21	19	15	14
Peak chick mass (kg)	0.25	0.75	1.25	1.25
Brooding time per parent (proportion of day)	0.5	0	0	0
Mean food load mass (g, wet mass)	12	25	200	250
Energy density of chick meal (kJ/g, wet mass)	5	5	7.2	7.2
Estimated from general regression (Friesen *et al.* 1989)				
Chick food requirement at peak mass (kJ/d)	245	600	797	797
Energy expenditure (kJ/h)				
Resting/brooding	28	28	28	28
Flying (multiple of resting)	3	2.8	2	1.5
Feeding (multiple of resting)	2.6	2.4	2	1.5

flight speed and the energetic cost of transport. We also investigate the relationship between colony size and foraging distance.

We investigated these questions for seabird adults in four classes, 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 h/d for foraging by each parent; these birds have a very high wing-loading (1.7–1.9 g/cm²)

- 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 forage 24 h/d; wing loading approximately 1.4 g/cm²

- A "shearwater type" (e.g. *Puffinus* spp.), having a flight combining flapping and gliding and a chick that is left unattended when large, allowing both parents to forage up to 24 h/d; wing loading approximately 0.9 g/cm²

- A "gadfly petrel type" (e.g. *Pterodroma* spp.) depending mainly on soaring flight and with both parents foraging up to 24 h/d; wing-loading approximately 0.7 g/cm²

Wing loading values were calculated from data in Tennekes (1996), corrected for allometry, as shown in Gaston (2004). To increase comparability, we used regression equations relating energy expenditure to body mass for different activities for adults, rather than published values for the energy expenditure of the selected genera. Table 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 the latter part of the growth period, include tropical species for which thermoregulation costs are likely negligible (Warham 1990). Nestling *Fratercula* at high-latitude colonies certainly would expend energy on thermoregulation, but to increase comparability, we omitted that factor here. Table 1 shows values assigned for the four genera.

Seabirds accumulate energy reserves in the form of lipid deposits, but most seabirds deliver food to nestlings in the form of unprocessed prey items (Gaston 2004). The cost of transport increases with total mass (body structure + lipid reserves + nestling food), and there is a limit above which the bird cannot become airborne. Most seabirds reduce their lipid reserves during chick-rearing, creating a compromise between the risk to their own survival and the demands of the optimal chick growth trajectory (Gaston & Hipfner 2006). This adjustment may be progressive during chick-rearing and may amount to 5%–10% of total energy expenditure on flight (Croll *et al.* 1991). However, we also have omitted this potential adjustment.

Energy balance

To develop the energy balance equation, we divide parental activity budgets into feeding (includes swimming and diving, and pauses between dives; indexed by subscript "f"), travel flight (indexed by subscript "t") and resting or brooding (indexed by subscript "r"). Each has a corresponding rate of energetic expenditure (e_f, e_t, e_r). The parent spends time t_f, t_t and t_r only on these three activities, which must sum to 24 hours.

In one case (*Uria*) the brooding time is also set, reducing the time available for foraging and travel. The key variable in the analyses is the distance to the foraging location, which in turn sets foraging time and the energy required. The energy balance equation is

$$R \cdot t_f = Y + (e_f \cdot t_f) + (e_t \cdot t_t) + (e_r \cdot t_r), \qquad (1)$$

where Y is the total daily delivery by each parent (in kJ), and R is the net feeding rate (kJ/h). This equation says that the total amount of energy captured by feeding for time t_f at rate R must equal the total amount of energy delivered (Y), plus that expended on the parent's three activity types. We assumed that the delivery by each parent was equal to half of the chick's energy needs, estimated at peak growth period. We varied that amount in some of our computations. The time spent travelling each day is the time required for each trip multiplied by the number of trips, which is

$$t_t = (2D/S) \cdot (Y/L), \qquad (2)$$

where D is the one-way distance travelled between colony and feeding area (in kilometres), S is flight speed (kilometres per hour), Y is the total daily delivery (equivalent to the nestling's daily energy need) and L is the load size delivered on each trip. We assume that the load size stays constant for a given species.

We ask first about the relative availability of prey at various distances from the colony that results when parents provision according to our assumptions of energy balance and delivery maximisation. We use equation 1 to calculate the feeding rate (R) that would be required at successively greater distances from the breeding colony to sustain a given delivery rate. Using the input parameters from Table 1, we first assign the required brooding time (if any), calculate the travel time required for increasingly distant trips from the colony, calculate the resultant feeding time, and calculate the feeding rate necessary to support the required delivery rate as a function of distance. Fig. 2 shows that a murre parent travelling 50 km from the colony requires a feeding rate of 147 kJ/h to achieve a delivery of 122.5 kJ/d (its share of the chick's peak requirement). In contrast, a parent travelling 100 km from the colony requires a feeding rate of 212 kJ/h to achieve the same delivery rate. A puffin, because it does not brood its nestling and because it can carry a larger food load, requires corresponding feeding rates of only 96 kJ/d and 124 kJ/d when travelling the same distances.
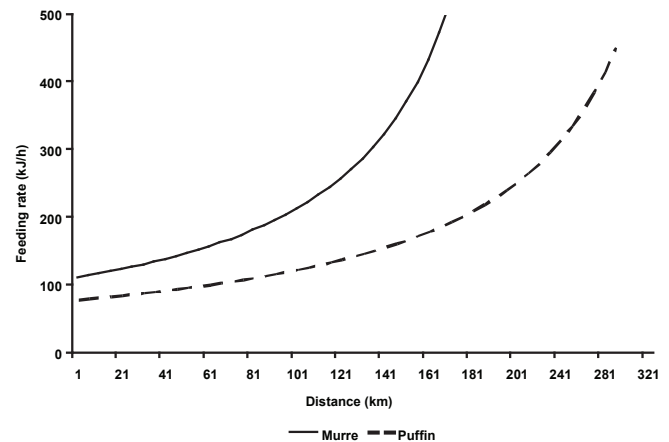
Fig. 2. Model predictions of the feeding rate required to achieve the necessary delivery rate for various travel distances for *Uria* and *Fratercula.* Table 1 gives the baseline parameters.

Fig. 3 shows the relationships between the required feeding rate and foraging range for all four model species. These curves are truncated because, as the travel time approaches the total time available, feeding time becomes very short, and hence the required 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" rate; see Table 2).

A strong contrast is evident between the auks and the petrels, with maximum foraging ranges for the latter exceeding that for the 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 back to the nestling in the form of stomach oil, giving it a higher energy value. Consequently, a shearwater could travel up to 1800 km from the colony to use a food source allowing a rate of food acquisition similar to a source that would constrain murres to within 100 km (213 kJ/h).

Within seabird species, the maximum size of the chick varies a great deal between years and between colonies (Gaston 1985). This variation has a large effect on the required daily delivery, which in turn affects the maximum foraging range. Fig. 4 illustrates the 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 to 400 km. The corresponding range for puffins is 222 km to 677 km (Fig. 4). Over the range from –50% to +50% of mean chick
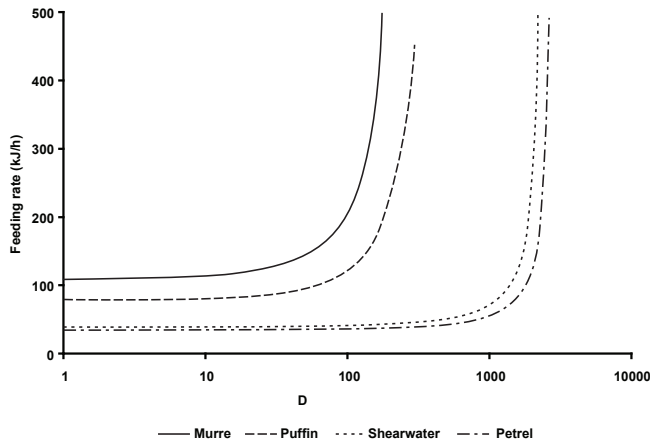
energy needs, the relationship between energy needs and maximum foraging range is steeper for *Uria* than for *Fratercula,* so that a given change in feeding rate enables a greater change in foraging range for the former, making flexibility in chick feeding rates a potentially more useful strategy for *Uria* than for *Fratercula.*

Colony size and foraging radius

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 that results from the feeding activities of the parents. Call the relationship between feeding rate and travel distance F(d). Feeding rate and prey density are related by the functional response, which is a well-studied phenomenon (e.g. Holling 1965, Anderson 2001, Weitz & Levin 2006), but we had to make an assumption about the intensity of foraging activity that a given density of prey could sustain throughout the breeding season. In reality, intensity is a complicated interaction between the functional response, the regeneration (growth and reproduction) capacity of the prey base, and the degree to which the prey base could allowably be reduced in the course of a breeding season. We compress all of this biology into an assumed, simple linear relationship between the sustainable density of feeding birds and F(d), symbolised by the coefficient α.

For the calculations used here, we set α to 0.01 bird•h•km^{-2}•kJ^{-1}, so that if, for example, F(d) is 62 kJ/h, then the prey base is on average able to sustain 0.62 actively feeding birds per km^2. If F(d) is 162 kJ/h, then the prey base is on average able to sustain 1.62 actively feeding birds per km^2, and so on. The general form of our results is remarkably insensitive to the value of α.

To find the colony size that can be sustained within a given foraging range, we computed the area of ocean in successive rings of five kilometres around the colony, and calculated the sustainable density of feeding birds in each. The number feeding there is the product of the sustainable density and area. In addition to the birds feeding in each ring at any one time, some birds are in transit between that ring and the colony. The number of birds in transit is related to the number feeding as the ratio of transit time to feeding time. The sum of the number of birds travelling and those feeding gives the number exploiting that particular ring.
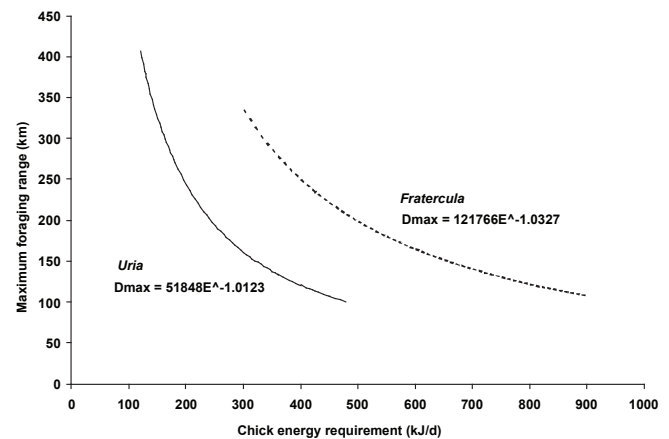

Fig. 3. Model predictions of the feeding rate required to achieve the necessary delivery rate, as a function of distance, for four basic seabird "types" modelled on the genera *Uria, Fratercula, Puffinus* and *Pterodroma*. Table 1 gives the baseline parameters.

TABLE 2
Maximum travel distances for two cases:
where maximum feeding rate is 5× basal, and
where maximum feeding rate is 10× basal

Multiple of basal acquisition rate	Maximum travel distance (km)			
	Uria	*Fratercula*	*Puffinus*	*Pterodroma*
5×	174	240	1860	2180
10×	198	272	2100	2460

Fig. 4. Model predictions for the effect of changes in chick energy requirements on foraging range. Table 1 gives the baseline parameters with the maximum feeding rate constrained at 10× basal feeding rate.

Figs. 5 and 6 show the results. The relationship between colony size 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 10 000 birds and at 192 km for colonies of 1 000 000 birds. These values encompass the range of foraging ranges observed for Thick-billed Murres *Uria lomvia* in the Canadian Arctic, where colonies fall within the same size range (Gaston 2004). Corresponding distances for *Pterodroma* are 700 km and 2040 km. Of course, the absolute values depend on our initial guesses, and consequently their reliability is unknown. However, the shape of the relationship does not depend on α and should be robust.

THE EVIDENCE

Actual empirical tests of the existence of Ashmole's halo have been very few. Birt *et al.* (1987) carried out surveys of bottom fish density in relation to distance from a colony of Double-crested Cormorants *Phalacrocorax auritus* and showed that the density increased with distance from the colony. Twenty years later, that survey remains the best direct evidence for the existence of the halo. Strong evidence is also provided by a recent study of foraging by Adélie Penguins *Pygoscelis adeliae* suggesting that cropping by the birds causes declines in local food abundance, forcing birds to feed progressively further from the colony (Ainley *et al.* 2004, 2006), Similar, but less direct evidence, is provided by studies of foraging among Thick-billed Murres, in whom depth and duration of dives made to provide food for nestlings was found to decrease with distance from the colony, indicating that feeding became easier, and presumably food denser, as birds travelled further from the colony (K. Elliott unpub. data).

Colony size may have an effect on reproductive success and chick growth, with larger colonies having lower success and growth rates than small ones ("the hungry horde effect," Cairns 1992). This type of within-species comparison has been considered to provide evidence for the existence of Ashmole's halo among temperate- and Arctic-breeding seabirds. However, no plausible explanation for why birds at large colonies, presumably indicative of superior conditions, should do worse than those at small colonies has been put forward. The effect is suggestive of density dependence affecting reproduction (Gaston *et al.* 1983, Hunt *et al.* 1986), but the lack of
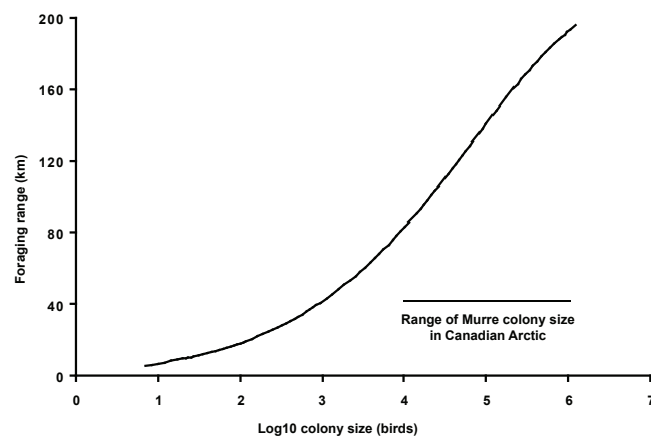
replication for other species suggests that the relationship may not be typical, and the observations remain enigmatic.

Similar circumstantial evidence for food competition around breeding colonies is provided by the distribution of colony size among certain British seabirds, suggesting that large colonies suppress the development of adjacent smaller colonies (Furness & Birkhead 1984). This interpretation has been criticised by Cairns (1989), who provided an alternative explanation based on differences in continental shelf areas available for foraging. However, similar evidence for competition among colonies resulting in over-dispersion was found by Ford *et al.* (2007) for colonies of Black-legged Kittiwakes *Rissa tridactyla* and by Ainley *et al.* (2004) for Adélie Penguins. Again, the exact cause of the effect is enigmatic, although it likely indicates competition for food during breeding.

Lewis *et al.* (2001) showed that Northern Gannets *Morus bassanus* breeding in large colonies travelled further to forage than did those from small colonies. That result accords with our model, but it falls short of providing proof either than intracolony competition is the cause or that the variation affects reproductive success. All Northern Gannet colonies are currently expanding (Moss *et al.* 2002), and so they do not necessarily represent a situation in which feeding constraints are having significant effects on reproduction. The results of Forero *et al.* (2002), who showed that birds from large Magellanic Penguin *Spheniscus magellanicus* colonies tend to feed at lower trophic levels than do birds from small colonies, and that the former have lower reproductive success are likewise suggestive of local food depletion. However, the finding that birds from large colonies feed closer to their breeding sites than do those from small colonies is hard to reconcile with food depletion, and so that result remains somewhat enigmatic.

Diamond (1978) provided a useful test of Ashmole's idea when he compared population sizes between resident and migratory seabirds breeding on tropical oceanic islands. He showed that, within genera, the populations of migratory species were generally much larger than those of resident species and that populations of migratory inshore feeders were larger than those of pelagic residents. These findings seemed to indicate that migration, presumably conferring a much larger potential foraging area, was a more important determinant of population size than was foraging range during
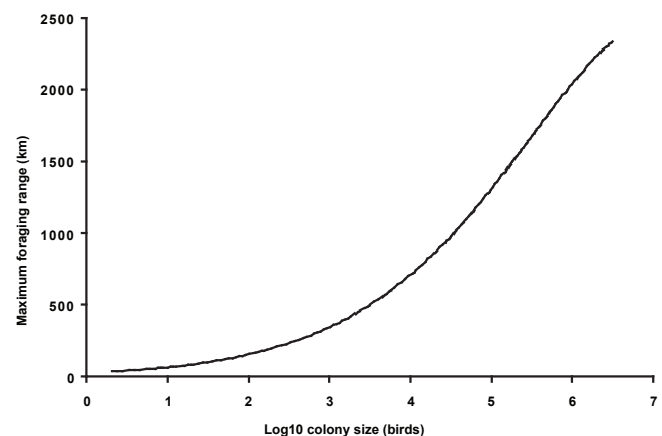

Fig. 5. Model prediction for the relationship between colony size and foraging range in *Uria.* Table 1 gives the baseline parameters, with the maximum feeding rate constrained at 10× basal feeding rate.

Fig. 6. Model prediction for the relationship between colony size and foraging range in *Pterodroma.* Table 1 gives the baseline parameters, with the maximum feeding rate constrained at 10× basal feeding rate.

breeding—apparent evidence for Lack's view. However, the outcome depended mainly on the difference between migratory 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.

DISCUSSION

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 predation (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 seabird prey (e.g. stocks of small fishes) tend to be much greater than do changes in the populations of marine birds (Cairns 1992). The apparent contradiction between traits characteristic of resource limitation on the one hand and observations of prey fluctuations and catastrophic adult mortality on the other is one that remains unresolved.

Lack (1966, 1968) considered that population regulation for seabirds probably occurred outside the breeding season. Studies of the timing of mortality in temperate seabirds seem to support that view, because most mortality seems to occur in winter (e.g. Meade 1974). However, those findings tell us nothing about 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 in determining population trajectory. Again, that finding does not indicate that populations are controlled by changes in adult survival—merely that population trajectories are strongly affected by changes in adult survival when they occur. For example, Harris *et al.* (2005) found that winter mortality did not account for demographic changes in Atlantic Puffin *Fratercula arctica* populations, despite the variations noted over the substantial range studied. If, in the real world, adult survival is rather stable as compared with other demographic variables, it may be relatively unimportant in determining population status.

Ashmole's hypothesis not only predicts limits to colony size, but also indicates the sort of selection under which the typical seabird life-history strategy could have evolved: As colonies expand, they create selection for reduction of the provisioning requirement. Our results demonstrate more explicitly how traits such as meal size, mediated by wing-loading and flight style and chick growth strategies, can affect potential foraging range and help to free seabirds from the land-dependence created by their terrestrial breeding constraint.

Our model results do not relate directly to Ashmole's halo, but rather describe the feeding rates that must be supported at a given feeding site to account for breeding birds foraging at such a distance from the colony. If food depletion actually occurs, then the limit of our distance-feeding rate relationships determines the maximum extent of the halo for a given species.

Our model demonstrates that, at food densities close to basal (i.e. conditions in which the existence of a colony is marginal), small variations in possible feeding rates may have large effects on foraging range. Conversely, where a colony is close to the foraging range-limit for the species, even large changes in potential feeding rate are unlikely to create detectable changes in foraging range. Those findings suggest that, for a given species, the presence of Ashmole's halo may be easier to detect for large colonies than for small ones. Likewise, the relatively small difference in predicted foraging range over a wide range of colony sizes, added to the difficulty and expense of measuring foraging range, suggest that correlations of colony size and foraging range are likely to provide only a crude test of our model results and hence only a weak demonstration of Ashmole's halo.

Some limitations to the current model need to be recognised:

- We have assumed that seabirds spend the whole of their time either foraging or (in the case of *Uria*) chick-guarding. In practice, social interactions, rest and maintenance activities will take up some time and hence reduce potential foraging range.

- As noted earlier, adaptive mass adjustments will affect food-carrying capacity, flight speed and energy expenditure, although the adjustments are not likely to be large as compared with the range of food acquisition rates considered here.

- Predation and parasitism may affect both adult time budgets and chick energy needs, and these factors are likely to vary considerably between colonies.

- It is worth noting that, although potential maximum foraging range is affected by flight speed, in practice the adjustment of flight speed is possible only within rather narrow limits, because each species' aerodynamic design has a characteristic V_{mr} [the speed that minimises energy expended by distance travelled (Pennycuick 1997, 1998; Rayner 1999, 2001). Murres, especially, seem to have little leeway for adjusting flight speed (Elliott & Gaston 2005).

Most previously presented evidence relating to the existence of Ashmole's halo has made use of intercolony comparisons (e.g. Furness & Birkhead 1984, Hunt *et al.* 1986, Lewis *et al.* 2001). However, in reality, intercolony variation in foraging range, breeding success and nestling growth rates probably relates to variation in local food availability, rather than to the activities of the birds themselves. Seabird populations, because of the longevity and philopatry of most breeders, tend to be relatively stable from year to year as compared with their food resources (Cairns 1992). Such variability means that the comparative approach is best employed either where populations are known to be in equilibrium, or where many colonies can be compared.

Likewise, the "hungry horde effect," which seems intuitively to relate to food depletion around large colonies, presumably results from adjustments to feeding rate made in the context of strong intraspecific competition. That interpretation raises the question of why birds in that situation do not emigrate. However, emigration presents its own problems: locating and assessing alternative breeding sites, and becoming familiar with foraging in foreign waters. At present, we cannot evaluate those costs. It may be that, in fitness terms, remaining with a suboptimal colony may be the best option for the individual even if it might not be the right option for the population.

CONCLUSIONS

Evidence from the ghost of past competition

The more or less universal reduction of clutch size to one egg among pelagic seabirds strongly suggests that, in the past, competition between

members of the colony with regard to feeding has been depressed to the point that food is available for rearing only one offspring annually (in some cases one every two years). Low fecundity would be a simple means by which seabird populations at the limit of their food supply could continue to reproduce (Ricklefs 1990)—a result predicted by Fig. 5. Observations of life-history traits in seabirds accord well with the predictions of Ashmole's hypothesis.

Further tests of Ashmole's hypothesis

The work of Lewis *et al.* (2001) and Ainley *et al.* (2006) on distance-dependant foraging behaviour seems to offer better evidence for the existence of Ashmole's halo than do intercolony comparisons of population dynamics or reproduction, which will almost certainly be confounded by environmental variability. A combination of the modelling approach used here and empirical observations of foraging effort should yield a more definitive answer to the importance of Ashmole's hypothesis in understanding seabird biology and evolution.

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